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Dr. John S. Stephens, Jr.
1932–2022

John S. Stephens, Jr. at his desk in the Moore Laboratory of Zoology.

John S. Stephens, Jr., James Irvine Professor of Environmental Biology Emeritus and founder of the Vantuna Research Group at Occidental College, passed away on June 5, 2022, he was 90. He spent 44 years as a teacher, mentor, and researcher in marine ecology, environmental biology, and ichthyology at Occidental, and continued his activities in research and advising until his death.

Growing up in the Los Angeles area, John developed an early interest in the ocean, which his wife, Nancy, said goes back to his pre-teen years at his grandparents' house in Hermosa Beach. In his teens, he and friends began participating in the new sport of SCUBA diving, using equipment that they themselves had constructed. He continued diving for most of the rest of his life (in his 60s, he finally obtained a certification card by asking the owners of his long-term dive shop, Dive N' Surf, to give him one; he needed it for an Army Corps of Engineer's contract to study the Portuguese Bend Landslide). He was one of the small cadre of marine biologists in the 1950s who pioneered the use of SCUBA in research.

John attended Stanford University as an undergraduate. One curious note about his time there is that he competed on the Stanford trampoline team (yes, there apparently was such a thing). He studied biology at Stanford, graduating in 1954. Some of us recall him saying that he was interested in reptiles at that time, an interest that he demonstrated on field trips to the desert for his Biology of the Vertebrates class. According to Nancy, however, his interest in the ocean led him to pursue marine biology and ichthyology. He earned Master's (1957) and Doctoral (1960) degrees at UCLA under the direction of Boyd

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Walker, conducting research on the taxonomy of chaenopsid blennies. He revised the family Chaenopsidae (Stephens 1963) and was always viewed as one of the leading worldwide experts on blennies. This research led to the bulk of his early publications. In 1978, he and Richard Rosenblatt named a "new and unusual" genus of chaenopsid blennies for John McCosker, who studied with both.

After a year as a teaching associate at U.C. Santa Barbara (1958–1959), John began his career at Occidental College in 1959, becoming an Assistant Professor in 1960. He was still less than 30 years of age. John held several important positions during his career. He was named James Irvine Professor of Environmental Biology in 1974, founded the Vantuna Research Group (VRG) that same year, served as Biology Department chair and Faculty Council president, and was awarded the Graham L. Sterling Memorial Award in 1979, the college's most prestigious faculty award.

John taught a number of courses over the years, but classes on vertebrates were his specialty. His course on the Comparative Anatomy of Vertebrates was a cornerstone for most Biology students, where, if they could keep up, they took pages and pages of notes, including attempts at copying John's two-handed, three-color, cross-sectional diagrams. In the lab, dissections were always interesting, and the practical exams challenging. As a reward to students after completing a practical exam (and in an instance of his sense of humor), he often cooked up food for the class from the type of animal they had just studied. Rich in information, Comparative Anatomy also offered a powerful integration of anatomy, embryology, and evolution that served for most students as a major conceptual step in their understanding of biology. His class on the Biology of Vertebrates served as an introduction to the systematics, characteristics, and ecology of the major groups of vertebrates. For many years, this was the closest to an ecology course offered at Oxy. Among the memorable features of this class were its many field trips to an array of habitats in Southern California. Some of us remember every single field trip made in that class, after decades. Other upper division courses included Biological Oceanography, Evolution, Fisheries Biology and, of course, Ichthyology.

John was an excellent classroom teacher, often mentioned in surveys of alumni as being among the most memorable teachers at Oxy. He offered troves of information and ideas, but he did it with humor and sometimes irreverence. He enjoyed mixing with students during labs, and always had an open door to answer questions or provide guidance about studying. He also wanted students to think on their own. His questions on essay exams often required students to apply ideas from class creatively; former students noted that the exams themselves were learning experiences. For some classes he had a list of a few books, beyond the textbook, that were related (often loosely) to the topic of the course, and asked students to read one of them, giving them the opportunity to explore knowledge in the field on their own. In Comparative Anatomy, one of us remembers John asking students to design one question of their own for the final exam, and then write an answer. Nowadays, this would be thought of as experiential learning, and maybe John thought of it like that. But maybe he thought it was a fun thing to do.

John established a research program at Occidental that was an exemplar of the small-college model, featuring extensive participation by undergraduate students. As his career developed, however, he built upon this model in a novel, larger-scale way. His earliest research at Oxy continued with blennies, focusing on the comparative ecology of three species of *Hypsoblennius.* Supported by NSF grants, this research led to a paper in Ecological Monographs (Stephens et al. 1970), one of the first theoretically-based papers from California that utilized SCUBA as a research tool. Three undergraduate students were

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co-authors on this paper, six additional undergraduate students were acknowledged for important contributions, and we know that other undergraduates, including some Biology of the Vertebrates classes, were also involved in data-gathering. At the same time, John supervised undergraduate research projects carried out by other undergraduate students on topics unrelated to the *Hypsoblennius* project. This engagement with undergraduate students in projects outside of class was something that carried through John's career.

But while the *Hypsoblennius* crew initially had to carry their SCUBA gear down the cliffs at Palos Verdes to reach their study sites, the range of the program expanded in the late 1960s with the acquisition of the *Oxyblennius*, a 17-foot Boston Whaler. A much greater change occurred in the late 1960's, when Occidental alumnus Gilbert Van Camp III, CEO of Van Camp Seafood Industries, donated his personal tuna fishing boat, the 85' *Vantuna* to the college. John was instrumental in arranging the donation, and procured a grant from NSF in 1969 to outfit the vessel for research.

The R/V Vantuna greatly expanded the range and scope of marine biology at Occidental. It became a platform for field trips by secondary and tertiary-level students from all over Southern California, in a program developed by John and Ruth LeBow of Pierce College. Undergraduate students from Occidental were the onboard instructors for around 150 trips per year, themselves learning field techniques, identification of marine organisms, teaching skills, and boat maintenance through their training and practice on the Vantuna. For more than a generation, this program, one of the most successful outreach programs in the history of the college, exposed thousands of students from Southern California to marine biology in a field setting.

The Vantuna also provided new opportunities for research under John's direction. In the early 1970s he obtained grants from the Southern California Coastal Water Research Project to study the biology of fishes in the Southern California Bight and from Sea Grant to study the fishes of Los Angeles Harbor, providing opportunities for research and employment by even more Occidental students. In 1974, John established a relationship with Southern California Edison to study the effects of thermal effluent from a power plant at King Harbor in Redondo Beach, a relationship which lasted until 1988. Also, in 1974 he established the Vantuna Research Group to coordinate the range of research and teaching activities being conducted by his group at Occidental. It is impossible to know the exact number, but hundreds of undergraduate students and dozens Master's students were involved in research and field instruction in this program for the remainder of John's career. The Vantuna Research Group also provided a home for post-doctoral and other post-graduate researchers. The Vantuna Research Group produced around 80 scientific papers and several technical reports from the early 1970s to the early 1990s. Topics included the effects of temperature and toxins on individual fishes, life histories and feeding habits, and the composition and distribution of fish faunas off Southern California.

Among the more remarkable achievements of John and the Vantuna Research Group was the establishment of long-term monitoring programs for fishes at King Harbor and Palos Verdes. These time-series, which are still ongoing and were originally published in the Bulletin (Terry and Stephens 1976), constitute the longest continuous studies of rocky reefs in the world. While this time series is still revealing temporal variation in fish communities, a 1994 paper was significant in revealing a major shift, perhaps related to a change in the Pacific Decadal Oscillation, in the late 1970s (Stephens et al. 1994) and early on his work was cited as some of the first evidence of climate change (Hughes 2000).

After retiring from teaching in 1993, John continued as director of the Vantuna Research Group until fully retiring in 1996. He remained as the Executive Director till his passing.

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During retirement, he began monitoring fish populations in the Merced River and Morro Bay and curated the fish collection at Morro Bay Museum of Natural History. His most recent publication was in 2021 on the fishes in Morro Bay (O'Leary et al. 2021). He continued analyzing fish population data, collaborating with other researchers and publishing until his death.

A member of the American Society of Ichthyologists and Herpetologists, the American Institute of Fishery Biologists and the Southern California Academy of Sciences, Stephens' scientific expertise was widely sought after. He served as an advisor to the National Marine Fisheries Service and the California Department of Fish and Game on such issues as the effects of man-made environments on fish and the impact of pollution on fisheries biology.

John had a big, magnetic personality. He was an accomplished scientist and leader, but he did not take himself very seriously. Early in his career, his staff and students dropped the Dr. Stephens moniker and he was simply known as 'Doc'. He had a great sense of humor, and enjoyed life. He liked participating in sports, rarely missing his weekly basketball game at Oxy, and continuing his basketball habits even after retirement. He loved skiing and golf, both of which were referred to as 'field work' and it was important to do them during the week. He liked travel, and even while working made time for long visits to Italy or Germany with his wife, Nancy. He liked red wine and grappa. He was irreverent, with a kind of "I don't need no stinking badges" attitude, and was known for his use of a hammer to resolve just about any mechanical problem, be it with an outboard motor or a regulator second stage. Doc like to refer to himself as a scuba diver who does science to justify the diving and clearly embodied the motto that if you want to learn something about the ocean you had to get out there. It seems to us that even when he was doing serious things, he was having fun, and that was what was important to him. His wife Nancy said that what he did wasn't a job for him, and that he led a life that he would have planned.

John influenced the lives of an uncountable number of students at Occidental, and that may be his greatest legacy. In tributes after his death, many people pointed out his influence on them, many stating that he changed the course of their lives. John often seemed to recognize qualities in people that they did not yet know they had. Sometimes he would ask a student to do something that they didn't think they knew how to do, but seemed to trust that the student would figure it out. It was fun, an adventure, for the students, and we think it was fun for John as well. At the same time, he was exceedingly generous with his time, always ready, thoughtful and patient to answer questions about classes, research or discuss career options. He was a kind, sweet, and gentle man, someone who was not fettered by prejudices regarding race and sex, at a time when this could not be said for many other professors. Many of his students went on to careers in marine science, but many others went on in other fields; all experienced the personal and intellectual growth made possible by an immersive experience in marine biology. One former student recounted that, on telling John that he was her mentor, John replied "I'm nobody's mentor." He was a mentor; he was and still is an inspiration.

—Ralph Larson, Dan Pondella and Milton Love

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Gyrodactylus, Fundulotrema, and *Salsuginus* Species (Monogenea) Infecting *Fundulus parvipinnis parvipinnis* (Osteichthyes: Fundulidae) in Central and Southern California Estuaries and Bays

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Abstract.—A survey of *Fundulus parvipinnis parvipinnis* from coastal waters of Central and Southern California for Monogenea revealed two new species of *Gyrodactylus* Nordmann, 1832, *Fundulotrema prolongis* (Hargis, 1955) (both Gyrodactylidae), and a new species of *Salsuginus* Beverley-Burton, 1984 (Ancyrocephalinae). *Gyrodactylus kalmanae* n. sp. and *F. prolongis* attached primarily to the fins and body surface. *Gyrodactylus parvipinni* n. sp. was on the gills, fins, and body surface and, in some fish, formed dense aggregations on tips of gill lamellae and at the base of fins. *Salsuginus californiensis* n. sp. attached between adjacent secondary lamellae of the gill filaments. Partial 18S and ITS region (ITS1/5.8/ITS2) sequence data for the two new species of *Gyrodactylus* linked distantly to species from estuarine and marine fishes, but for *F. prolongis* were 100% and 99.88% similar, respectively, to samples from *Fundulus heteroclitus* in eastern North America. *Salsuginus californiensis* n. sp. differs from 11 previously described species of the genus in features of the accessory piece of the male copulatory organ and details of the larval hooks, with the molecular data reported herein being the first for this genus. The occurrence of *Salsuginus* from coastal California and western Mexico suggests this genus occurred on ancestral fundulids prior to isolation of Pacific species from eastern relatives by the Isthmus of Panama, estimated at 3 to 3.5 mya. Whether *G. parvipinni* n. sp. and *G. kalmanae* n. sp. have origins on ancestral fundulids or were acquired from local hosts after isolation is unclear at this time, but both species appear unrelated to species of *Gyrodactylus* from fundulids on the east coast. The finding of *F. prolongis* in California with almost identical 18S and ITS regions to eastern populations raises the question of its origin. Given the morphological and genetic similarities with populations on the east coast, *F. prolongis* (reported from a variety of eastern fundulid and related hosts) may have arrived via several related eastern host species introduced to and established in the state. If so, *F. prolongis* is a non-native species.

The Fundulidae (killifishes) are found in freshwater, brackish and marine habitats throughout much of North America and several Caribbean islands, with an estimated 43 fish species (Fricke et al. 2022). Two species are endemic to the Pacific drainage of California. The Baja California killifish (*Fundulus lima* Vaillant, 1894) occurs inland at several oases on the Baja Peninsula, while the California killifish (*Fundulus parvipinnis* Girard, 1854) inhabits coastal waters of California and the Baja Peninsula (Love 2011). The latter

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Table 1. Collection dates and localities from North to South of sampled *Fundulus p. parvipinnis* in Central and Southern California, U.S.A.

Locality	Longitude/Latitude[1]	Collection Date
Morro Bay	34.34359°, −120.84141°	6 Nov. 2022
Mugu Naval Air Station wetland, Ventura	34.105630°, −119.126278°	23 Sept. 2021
		1 April 2022
Seal Beach Naval Weapons Station/National	33.745622°, −118.085421°	10 Sept. 2021
Wildlife Refuge wetland, Anaheim Bay	33.745053°, −118.073435°	24 March 2022
San Dieguito Lagoon Del Mar	32.968205°, −117.250195°	12 Jan 2021
Rose Creek, Mission Bay, San Diego	32.804802°, −117.222766°	15 June 2021
Mission Bay, San Diego	32.769276°, −117.210344°	15 June 2021
F/G Street Tidal Creek, San Diego Bay[2]	32.631422°, −117.104457°	25 March 2021
		22 April 2021
		4 June 2021
		15 June 2021
		1 April 2022
Emory Cove Marsh, San Diego Bay	32.602591°, −117.123368°	2 April 2022
Crown Cove area, San Diego Bay	32.634714°, −117.138009°	4 Oct 2021
		29 June 2022

[1] Based on Google Earth Pro.
[2] Type locality.

fish is classified into two subspecies, *F. p. parvipinnis* (Morro Bay, California to Punta Eugenia, Baja California Sur) and *F. p. brevis* (Punta Eugenia to Almejas Bay, Baja California Sur) (Bernardi et al. 2007). Non endemic fundulids reported from the Pacific Coast include the rainwater killifish [*Lucania parva* (Baird and Girard, 1855)], with established populations in the San Francisco Bay estuary and Irvine Lake in Southern California (Fuller et al. 1999; Fuller and Neilson 2022), and the bluefin killifish (*L. goodie* Jordan, 1880) which is present in the San Francisco Bay area and San Dieguito estuary in Southern California (O'Rear et al. 2020; Fuller 2022).

Previous parasite surveys of *Fundulus* (see Hoffman 1999; Harris and Vogelbein 2006; King and Cone 2009) report a diverse group of viviparous Monogenea, including *Gyrodactylus* (4 species), *Fundulotrema* Kritsky and Thatcher, 1977 (6 species), and *Swingleus* Rogers, 1969 (2 species). The list also includes oviparous *Salsuginus* Beverley-Burton, 1984 (6 species). Most records are from host fishes east of the Rockies to the Gulf and Atlantic coasts. To date, little information is available on these ectoparasites from west coast killifishes of North America (Mizelle and Kritsky 1967; Harris and Vogelbein 2006). A single, unidentified species of *Salsuginus* has been reported from *F. lima* on the Baja Peninsula (Méndez et al. 2010).

Herein we describe *Gyrodactylus parvipinni* n. sp., *Gyrodactylus kalmanae* n. sp., *Salsuginus californiensis* n. sp., and document a first record of *Fundulotrema prolongis* (Hargis, 1955), all from *Fundulus p. parvipinis* from coastal waters of Central and Southern California. We included morphology, sequence data, and discussion of possible historical relationships with similar species described from fundulids in eastern North America.

Materials and Methods

Fundulus p. parvipinnis were collected by beach seine or minnow trap at various localities in Central and Southern California (Table 1). Fish were brought to the

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laboratory for processing within 48 hr of capture and were euthanized with tricaine methane sulfate (MS222) prior to examination in accordance with American Veterinary Medical Association Guidelines for the Euthanasia of Animals: 2020 Edition. Prior to euthanasia, fish were held in small, aerated aquaria containing water from the collecting site.

The descriptions are based on examination of specimens fixed with hot AFA, hot water with subsequent storage in 10% formalin, specimens fixed *in situ* with 10% formalin or after freezing, which relaxed the specimens. Live specimens, studied in temporary water mounts and examined with bright field and phase contrast optics, proved useful for viewing the digestive and reproductive organs and critical features of the haptoral hard parts. A few living specimens were placed in temporary mounts of sodium dodecyl sulphate (SDS) (Wong et al. 2006) to see details of the haptoral hard parts. Heat fixed specimens and *in situ* samples were stained in Mayer's acetocarmine, de-stained with 70% ethanol/5% vinegar, dehydrated in ethanol, cleared in clove oil, and mounted in Canada balsam. Relaxed, fixed specimens were stained for 5 min with Gomori's Trichrome (Kritsky et al. 1978) and cleared/mounted in a 50:50 glycerol/water mix; after several months the slides were soaked in tap water for 1 hr, the coverslips removed, and specimens processed as described for balsam mounts. Measurements for the gyrodactylids follow Malmberg (1970) but we refer to total length of the ventral bar instead of the total width of the ventral bar. For *Salsuginus* we followed Murith and Beverley-Burton (1985). Descriptive measurements are presented in μm as a mean followed in parentheses by range. Line drawings were made from a combination of scanned drawings made with the aid of a drawing tube or digital photographs, which were imported into Adobe Illustrator CS5, Version 15.1.0 for "inking."

Specimens of each species were identified in wet mounts. Individual worms were placed in microcentrifuge tubes, followed by DNA extraction using a Qiagen DNeasy Extraction Kit. Separate PCR reactions targeting the 18S rRNA gene and ITS1/5.8S/ITS2 region (ITS) of the gyrodactylids were completed using primers PBS18SF & PBS18SR (Cone et al. 2010) and P3b and P4 (Cable et al. 1999; Cable et al. 2005), respectively. For the *Salsuginus* specimens, the 18S rRNA gene and 28S rRNA genes were targeted using primers 81 and 83 (Mariaux 1998) and C1 & D2 (Chisholm et al. 2001), respectively. All primer pairs utilized a 53 μl of extracted DNA processed using the following thermocycler conditions: 95 °C for 10 min; 40 cycles of 95 °C for 1 min, 53 °C for 1 min, 72 °C for 2 min; 72 °C for 10 min. PCR products were purified and sequenced by Eton Biosciences (Union, NJ). The resulting sequences were examined and edited using Geneious Prime 2021.1 (www.geneious.com) and then queried through a BLAST search to find similar sequences (https://blast.ncbi.nlm.nih.gov/Blast.cg). Identification of the different regions of the ITS were determined using the labeled sequence presented in Cable et al. (1999). Type specimens of *Salsuginus bermudae* Rand and Wiles, 1987 (USNM 1375009), *S. cubensis* Mendoza-Franco, Vidal Martinez, Cruz-Quintana and Prats-Leon, 2006 (USNM 1392134), *S. neotropicalis* Mendoza-Franco and Vidal-Martinez, 2001 (USNM 1385225), *S. spirae* (Williams, 1980) (USNM 1371669; under synonym *Ancyrocephalus spirae*), *S. umbraensis* (Mizelle, 1938) (USNM 1321888), and *S. bahamianus* (Hanek and Fernando, 1972) (USNM 1368015) housed by the U.S. National Museum of Natural History (Smithsonian Institution, Washington, D. C.) (USNM), were examined. All fish names follow FishBase (Froese and Pauly 2022). Types and vouchers mounted on slides were deposited in the the USNM and Cabrillo Marine Aquarium (CMA).

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Results

Gyrodactylus parvipinni n. sp.

(Figs. 1, 2A)

The following description is based on 5 specimens.

Body 274 (220-380) long; 80 (68-88) wide at mid-body. Prohaptor bilobed, each lobe containing mass of terminal gland ducts; small spike sensilla seen occasionally. Cephalic gland cells lateral and posterolateral to pharynx. Pharynx 23 (22-31) in overall length, with smaller anterior bulb. Lateral bladders not prominent. Male copulatory organ (MCO) immediately posterior to pharynx, spherical, 10 (8.5-11) wide, with 1 large spine and 4 small spines in one arched row; small seminal vesicle present at base of MCO. Vas deferens not evident. Intestinal crura blind. Ovary round. Testis round, dorsal and slightly posterior to ovary. Haptor almost circular in ventral view, 55 (44-62) long, with smooth, non-pedunculate margin. Anchors 38 (36-46) in total length; root bent slightly medially, 9 (7-13) long; shaft 30 (28-33) long; point 16 (14-18) long. Ventral bar 26 (23-30) in total length, 16 (14-18) in transverse length; medial length 4 (3-5); anterolateral processes broad, 8.5 (7.5-9) long; ventral bar membrane well-developed, 14 (9-19) long, with distinct longitudinal ridges and slightly curved, thin posterio edge. Dorsal bar tube-like, often irregular in outline, 14 long, 2 wide medially, with a medial notch and two lateral protuberances seen in some specimens. Marginal hook 21.5 (20-24) in total length; handle 17 (16-18) long, with slightly rounded distal end in lateral view. Marginal hook sickle 4.5 (4-5) long; 3.5 (3-4.5) wide proximally, 3 (3-3.5) wide distally, with distinct toe and heel. Filament loop 7.5 (7-8) long.

Type host: Fundulus parvipinnis parvipinnis.

Type locality: F/G Street Marsh tidal stream, San Diego Bay, CA (Table 1).

Other localities: This species was present at all collection sites (Table 1).

Location: Gill lamellae and base of fins. The parasite attached mostly to the distal third of the primary lamellae and was the only gyrodactylid found on the gills. In some fish, the parasite occurred in dense aggregations (up to three or four dozen) at the base of the fins, peduncle, and tip of gill filaments where localized hyperplasia was evident when compared to an adjacent parasite-free filament (Fig. 2D-E).

Type specimens: The holotype (USNM 1684296) and paratype slides (USNM 1684297-1684299); paratype slide (CMA 2023.03.0001).

Etymology: This species is named after the host species, *F. p. parvipinnis*.

Molecular data: Sequence data for the 18S rRNA gene (455 bp; Accession OQ832326) and ITS Region (987 bp; Accession OQ832331) have been submitted to Genbank.

Remarks. Morphologically, *G. parvipinni* n. sp. resembles several gyrodactylids from leuciscid and moxostomid fishes in the southern U.S. in having a well-developed ventral bar with large, broad anterolateral processes, and a long striated posterior membrane, anchors with moderately developed roots, a marginal hook sickle with a relative long, thin handle, and a MCO having 1 large spine and 4-6 small spines similar in size in a single row. This group includes *G. alabamensis* Rogers, 1968 from bluehead chub (*Nocomis leptocephalus* (Girard, 1856)) in Alabama, *G. asperus* Rogers, 1967 from rough shiner (*Notropis baileyi* Suttkus and Raney, 1955) in Alabama, *G. magniclypeus* Rogers, 1968 from blacktip jumprock (*Moxostoma cervinum* (Cope, 1868)) in Virginia, and *G. tennesseensis* Rogers, 1968 from southern redbelly dace (*Chrosomus erythrogaster* (Rafinesque, 1820)) in Tennessee. In each case there are recognizable differences in the individual haptoral components and the MCO, with size of the anchors and ventral bar components of *G. parvip-*

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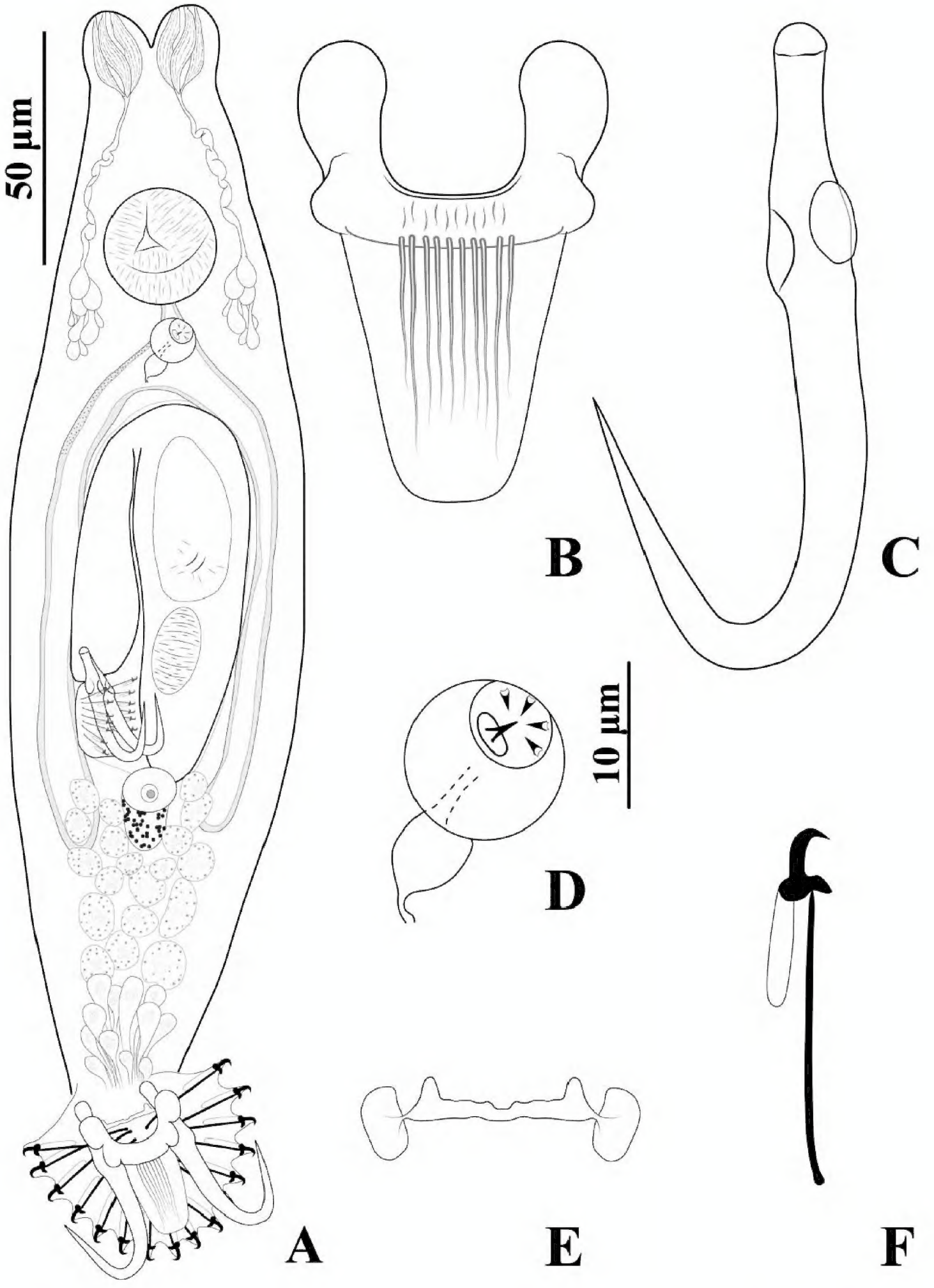

Fig. 1. Line drawings of *Gyrodactylus parvipinni* n. sp. from *Fundulus p. parvipinnis* from California. A. Body in ventral view. B. Ventral bar and membrane. C. Anchor. D. Male copulatory organ. E. Dorsal bar. F. Marginal hook.

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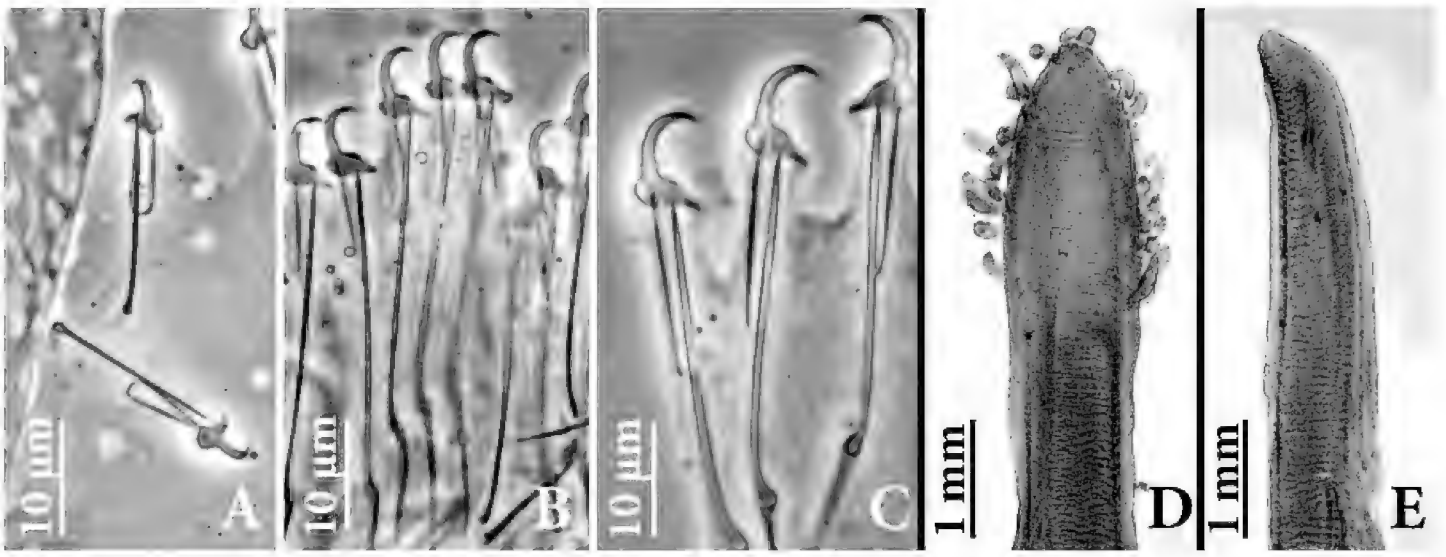

Fig. 2. Photographs of marginal hooks (A-C) of *Gyrodactylus* spp. and gill lamellae (D-E) from *Fundulus p. parvipinnis* from California. A. *Gyrodactylus parvipini* n. sp. B. *Gyrodactylus kalmani* n. sp. and C. *Gyrocatylus prolongis.*. D. Aggregations of *G. parvipini* n. sp. infecting a single gill lamella showing the characteristic hyperplastic tip. E. Non-infected gill lamella adjacent to the infected lamella.

inni n. sp. being noticeably smaller than those of the other species. *Gyrodactylus parvipinni* n. sp. does have haptoral and MCO features like *Gyrodactylus zapoteco* García-Vásquez, Pinacho-Pinacho, Martínez-Ramírez, and Rubio-Godoy, 2018 from Oaxaca killifish (*Profundulus oaxacae* (Meek, 1902)) in Pacific drainage streams of southern Mexico, but the latter species has a much shorter, stunted ventral bar membrane and a relatively thin, elongated sickle blade (García-Vásquez et al. 2018).

Molecular comparison with available sequences in GenBank did not identify any close similarity with either the 18S rRNA gene or the ITS region. The BLAST result with the top score in Genbank for the 18S rRNA gene was a *Gyrodactylus* sp. from the South American catfish (*Rhamdia quelen* (Quoy and Gaimard, 1824)) (Ictaluridae) from South America (87.28% similarity; e-value = 4e-142; Accession: MT521663.1). A BLAST search of the ITS region for *G. parvipinni* n. sp. resulted in the sequence with the top score being *Swingleus ancistrus* Billeter, Klink, and Maugel, 2000 from mummichog (*Fundulus heteroclitus* (Linnaeus, 1766)) (84.45% similarity; e-value = 3e-156), although the entry with the highest similarity was a Norwegian sample of *Gyrodactylus arcuatus* Bychowsky, 1933) (host: three spined stickleback (*Gasterosteus aculeatus* (Linnaeus, 1758)) (Gasterosteidae); 96.20% similarity; e-value = 7e-103; Accession: JN703797.1). A closer examination of *G. arcuatus* revealed the similarity was primarily associated with the 5.8S rRNA gene. Further analysis targeting the ITS1 (425 bp) revealed no significant similarity with any sequences in GenBank and the top matches for the ITS2 (407 bp) all shared less than 78% similarity. Additionally, a direct BLAST search comparing the ITS region of *G. parvipinni* n. sp. with that of *G. zapoteco* showed the two species were 92.83% similar, with this relationship confined to the 5.8S rRNA gene. It would appear *G. parvipinni* n. sp. is quite distant from North American coastal species described thus far with sequence data although there is sparse sequence data for gyrodactylids from North America in GenBank.

Gyrodactylus kalmanae n. sp.

(Figs. 2B, 3)

The following description is based on five specimens.

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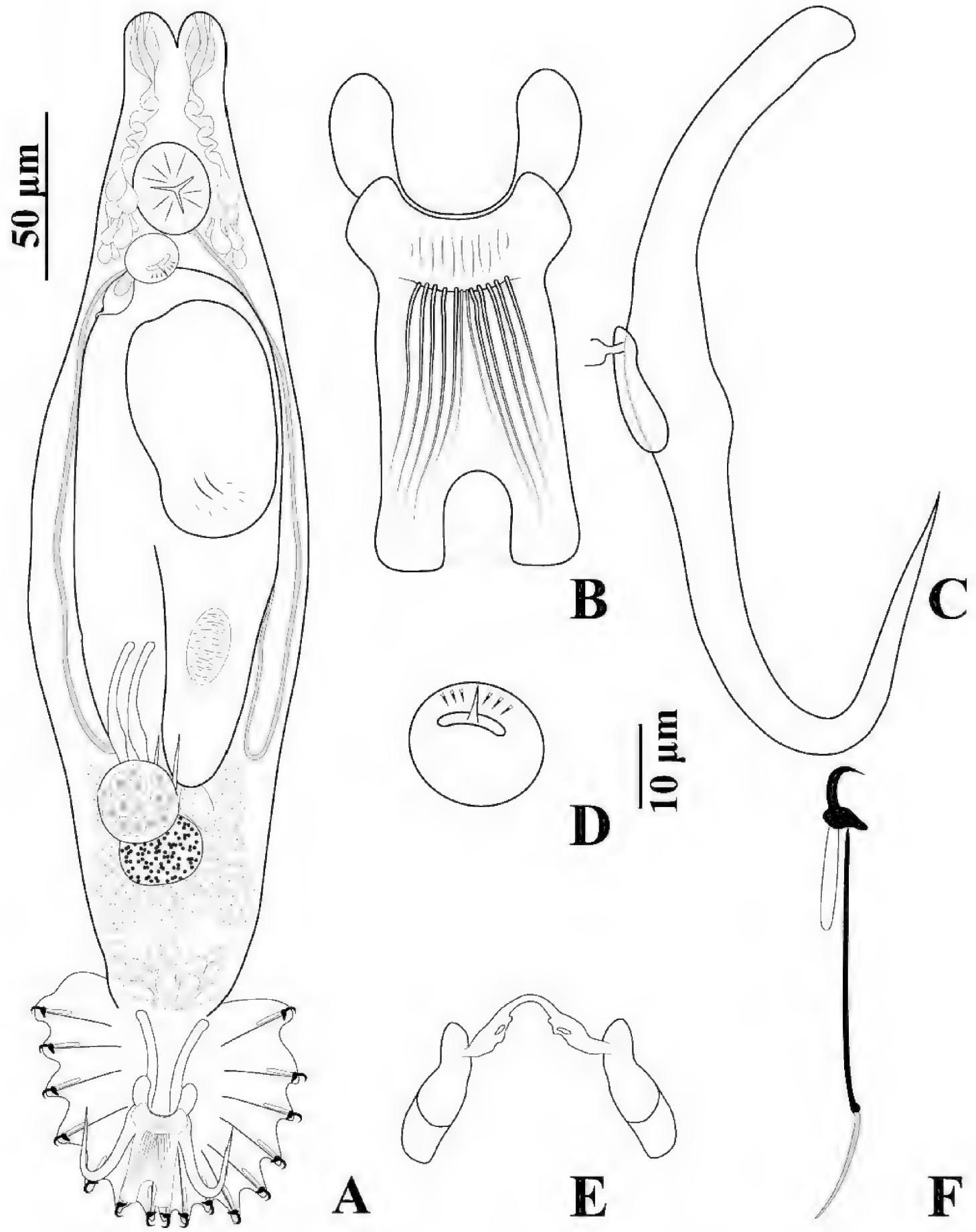

Fig. 3. Line drawings of *Gyrodactylus kalmanae* n. sp. from *Fundulus p. parvipinnis* from California. A. Body in ventral view. B. Ventral bar and membrane. C. Anchor. D. Male copulatory organ. E. Dorsal bar. F. Marginal hook.

Body 382 (342-406) long; 76 (73-82) wide at mid-body. Prohaptor bilobed, each lobe containing mass of terminal gland ducts; small spike sensilla visible in some specimens. Cephalic gland cells lateral and posterolateral to pharynx. Pharynx 25 long, with smaller anterior bulb. Lateral bladders not evident. Male copulatory organ (MCO) spherical, 15 (13-16) wide, immediately posterior to pharynx, with 1 large spine and 6 small spines in one

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arched row. Seminal vesicle prominent, immediately posterior to the MCO. Vas deferens not evident. Intestinal crura blind, ending near short peduncle. Ovary round. Testis round, dorsal to ovary. Haptor circular in ventral view, 119 (118-120) long, with a smooth margin incorporating the marginal hook sickles. Anchors 95 (92-98) long; root well-developed, curved, 48 (42-57); shaft 56 (54-58); point 31 (28-32). Ventral bar 66 (64-67) in total length, 33 (31-37) in transverse length; medial length 9; anterolateral processes prominent, 12.5 (12-13) long; ventral bar membrane well-developed, rectangular, 40 (38-41) long, with distinct longitudinal ridges and a slightly flared, flat and medially thinned terminal edge appearing indented. Dorsal bar tube-like, slightly irregular in thickness, 16.5 (11-21) long, 1 wide medially, and typically folded. Marginal hook 35 (30-35) in total length; handle 29 (26-33) long, with slightly flattened distal end and prominent ligament. Marginal hook sickle 6 (5-7) long, 3.7 (3-5) wide proximally, 3.5 (3-5) wide distally, with a finger-like toe and small heel. Filament loop 17.5 (17-18) long.

Type host: Fundulus parvipinnis parvipinnis

Type locality: F/G Street Marsh tidal stream, San Diego Bay, California (Table 1)

Other localities: Mugu Lagoon; Seal Beach National Wildlife Refuge; San Dieguito Lagoon; Rose Creek, Mission Bay; Emory Cove, San Diego Bay (Table 1).

Type specimens: Holotype slide (USNM 1684300); paratype slides (USNM 1684301-1684304); paratype slide (CMA 2023.03.0002).

Location: Body surface and fins.

Molecular data: Sequence data for the 18S rRNA gene (464 bp; Accession: OQ832324) and ITS Region (910 bp; Accession OQ832325) have been submitted to GenBank.

Etymology: This species is named for Dr. Julianne Kalman-Passarelli of the Cabrillo Marine Aquarium for her contributions to the biology of fish ectoparasites and to marine science education.

Remarks: Gyrodactylus kalmanae n. sp. has relatively large anchors with huge, extended and curved roots, and a similarly large ventral bar with broad well-developed anterolateral processes and a large, posterior membrane containing two prominent and diverging groups of longitudinal ridges, an MCO with a single large spine and up to 6 small, similarly-sized spines in 1 arched row, and a marginal hook sickle with a distinct toe and compact sickle blade and long thin sickle handle. These characteristics are seen in such species as *Gyrodactylus rhinichthius* Wood and Mizelle, 1957 from speckled dace [*Rhinichthys osculus* (Girard, 1856)] in Nevada, *Gyrodactylus spathulatus* Mueller, 1936 and *Gyrodactylus stunkardi* Kritsky and Mizelle, 1968 from catostomids in central and eastern North America (Beverley-Burton, 1984). With *G. spathulatus* and *G. stunkardi* both have a ventral bar membrane with an indentation at midlength and with the bar ridges extending only halfway along the membrane length. With G. *rhinichthius* the ventral bar has a distinct anterior medial knob, and the membrane ridges extend halfway. In *G. kalmanae* n. sp. the ventral bar does not have an anterior knob, and the membrane ridges extend almost the full length of the membrane, diverging into two lateral groups bending around the terminal excavation. The shared characteristics of this group also occur in species of *Fundulotrema* Kritsky and Thatcher, 1977 which differ from *G. kalmanae* n. sp. and the others in having unevenly distributed marginal hook sickles and the presence of a peduncular bar.

A search for similar sequences in GenBank with the 18S rRNA sequence data from *G. kalmanae* n. sp. showed an 85.92% similarity with *Gyrodactylus curemae* Conroy and Conroy, 1985 (Accession: MT521662.1; e-value = 8e-134; host: white mullet (*Mugil curema* Valenciennes, 1836). All other results had higher e-values. Analysis of the ITS region resulted in the highest score with *Gyrodactylus colemanensis* Mizelle and Kritsky, 1967

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(Accession: JF836142.1; 83.37% similar; e-value = 4e-110; host: brook trout (*Salvelinus fontinalis* (Mitchill, 1814)), although the species with the highest similarity was *Gyrodactylus marinus* Bychowsky and Poljansky, 1953 (Accession: GQ150537.1; 94.56% similar; e-value = 8e-97; host: Atlantic cod (*Gadus morhua* Linnaeus, 1758), with this similarity primarily occurring in the ITS1 region. The lack of any close match may reflect the sparse sequence data for gyrodactylids from North America in GenBank. It is noteworthy that sequence data from both *G. parvipinni* n. sp. and *G. kalmanae* n. sp. were significantly different from *Gyrodactylus stephanus* Mueller, 1937, a common parasite of *Fundulus* spp. from the east coast of North America, which suggest they have separate origins within this speciose genus.

Fundulotrema prolongis (Hargis, 1955)

(Figs. 2C, 4)

The following description is based on 5 specimens.

Body 426 (396-470) long; 87 (62-107 wide at mid-body. Prohaptor bilobed, each lobe containing mass of terminal gland ducts; small spike sensilla visible in some specimens. Cephalic gland cells lateral and posterolateral to pharynx. Pharynx 23 (20-31) in overall length, with small anterior bulb. Lateral excretory bladders not prominent. Male copulatory organ (MCO) spherical, 18 (15-21) wide, immediately posterior to pharynx, with 1 large spine with a relatively large base; 6 small terminal spines in one arched row. Vas deferens and seminal vesicle at base of MCO not evident. Intestinal crura blind. Ovary midbody, round in ventral view. Testis round in ventral view, dorsal and slightly posterior to ovary. Peduncular bar 66 (63-69) in transverse length and 20 (19-22) thick medially, with 31-38 elongate pits of varying length on anterior margin. Haptor rectangular in ventral view, 92 (61-101) long, with a smooth margin incorporating the marginal hook sickles. Anchors 83 (81-84) long; root well-developed, curved, 43 (37-46); shaft 47 (46-49); point 26 (23-30)]. Ventral bar 58 (56-60) in total length; 9 (8-10) in medial width, 29 (25-35) in transverse length, with a rounded anteriorly directed medial knob; anterolateral processes prominent, 11.5 (11-12) long; ventral bar membrane well-developed 34 (33-35) and appearing bifurcate, with distinct lateral longitudinal ridges and a slightly flared, flat and thinned terminal edge appearing as a medial excavation. Dorsal bar tube-like, tapering medially and typically folded anteriorly, 14 (11-17) long and 1 (1) thick, with small medial notch. Marginal hooks distributed unevenly around the haptoral perimeter, with three anterior pairs forming two anterior groups. Marginal hook 38 (36-40) in total length; handle thin along entire length, 29 (28-31) long with a small terminal swelling and prominent ligament. Marginal hook sickle with sloped toe, small heel, and straight shaft and curved tip; 7.5 (7-8) long; 4.5 (4.5-5) wide proximally; 4 (4) wide distally; filament loop 11 (9-13) long.

Host: Fundulus parvipinnis parvipinnis

Localities: San Dieguito Lagoon; F/G Street Marsh, San Diego Bay, Mugu Lagoon (Table 1).

Site: Body surface and fins.

Voucher specimens: Voucher slide (USNM 1684305-1684306) voucher slide (CMA 2023.03.0003).

Molecular data: Molecular data: Sequence data for the 18S rRNA gene (423 bp) and ITS Region (868 bp) were submitted to Genbank (Accessions: OQ830498 and OQ830563).

Remarks: The Californian samples were morphologically similar to previous descriptions of *F. prolongis* from fundulid hosts in central and eastern North America (Wellborn

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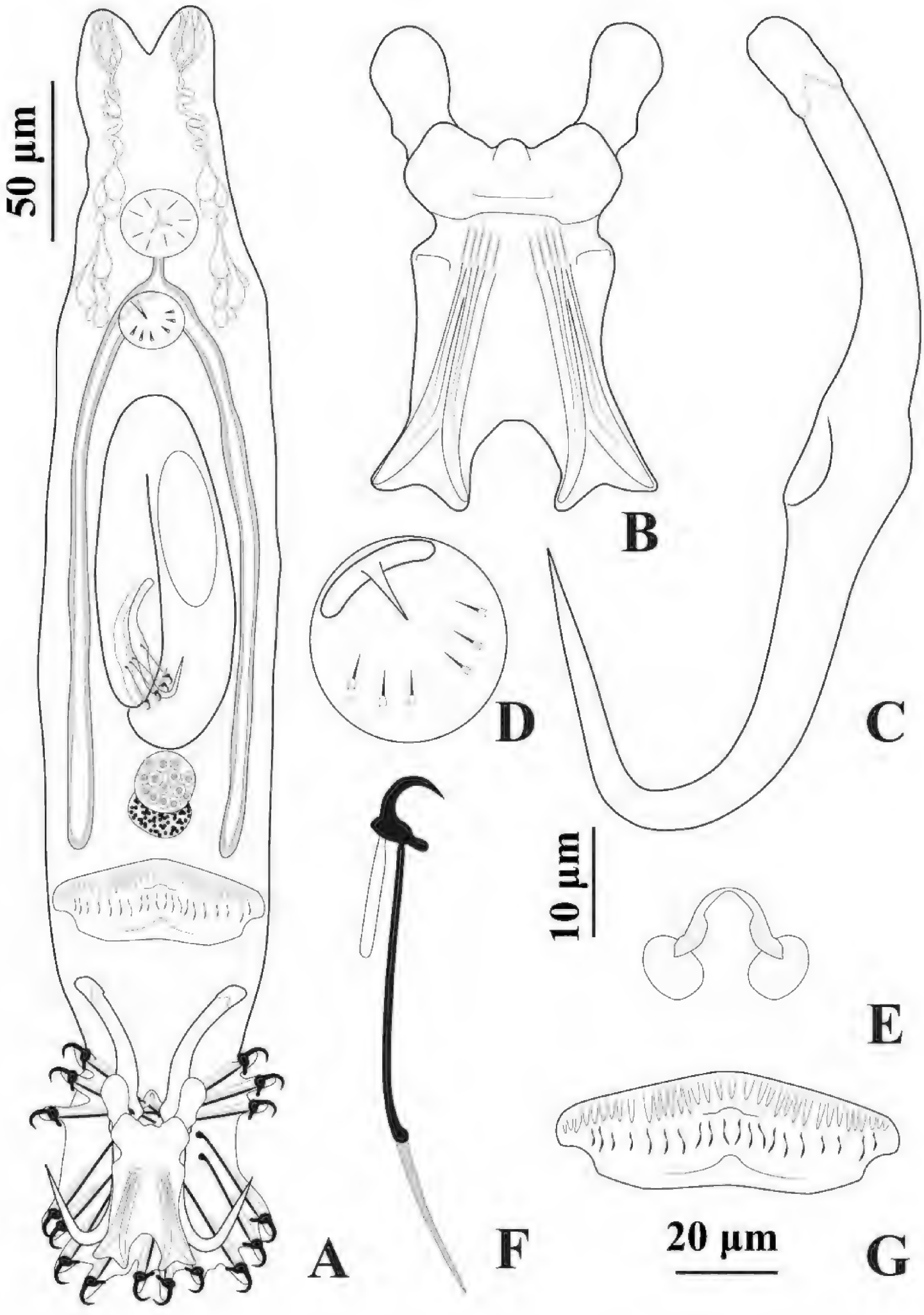

Fig. 4. Line drawings of *Fundulotrema prolongis* (Hargis, 1955) from *Fundulus p. parvipinnis*. A. Body in ventral view. B. Ventral bar and membrane. C. Anchor. D. Male copulatory organ. E. Dorsal bar. F. Marginal hook. G. Peduncular bar.

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and Rogers 1967; Williams and Rogers 1971; Dickinson and Threlfall 1975; Cone and Odense 1988). The present study extends the known range of *F. prolongis* from freshwater and coastal habitats east of the Rockies to host populations of *F. p. parvipinnis* on the Pacific coast. Previous reports include Gulf killifish (*Fundulus grandis* Baird and Girard, 1853) in Florida (Hargis 1955), banded killifish (*Fundulus diaphanus* (Lesueur, 1817)), in fresh waters of Nova Scotia (King and Cone 2009) and Ontario (Hanek and Fernando 1971), *F. heteroclitus* in coastal Newfoundland (Dickinson and Threlfall 1975), red river pupfish (*Cyprinodon rubrofluviatilis* Fowler, 1916) in Texas (McAllister et al. 2019a), and sheepshead minnow (*Cyprinodon variegatus* Lacepède, 1803) in coastal Alabama (Williams and Rogers 1971).

Sequence data of the 18S rRNA sequence (423 bp) were identical to *F. prolongis* from *F. heteroclitus* in Maryland, USA (HF548673.1; e value = 0) and Nova Scotia, Canada (JF836108.1; e value = 0) as well as a 97.4% match to *S. ancistrus* (HF548675.1; e value = 0) from *F. heteroclitus* in brackish water in eastern North America. Analysis targeting the complete ITS region showed the California specimens were 99.88% similar to *F. prolongis* (under synonym: *G. prolongis*; GQ918279.1; e value = 0) collected from *F. heteroclitus*, 95.71% similar to *S. ancistrus* from *F. heteroclitus* in Maryland, USA (HF548674.2; e value = 0), 88.71% similar to *F. foxi* (Rawson, 1973) collected from Canada (under synonym: *G. foxi*; GQ918278.1; e value = 0), and 95.42% similar to *Fundulotrema stableri* (Hathaway and Herlevich, 1973) collected from northern plains killifish (*Fundulus kansae* Garman, 1895) in Colorado, USA (AY099505.1; e value = 0). Since several of the related taxa only had ITS2 sequence data available, we also did a BLAST search targeting this region (386 bp). This search revealed similar matches to most of the same species: *F. prolongis* (under synonym: *G. prolongis*; 99.74%; e value = 0; GQ918279.1), *S. ancistrus* (96.38%; e value = 8e-178; HF548674.2), *F. stableri* (94.85%; e value = 2e-168; AY099505.1), *F. foxi* (under synonym: *G. foxi*; 86.86%; e value = 1e-115; GQ918278.1), as well as *F. porterensis* (84.67%; e value = 3e-67; FJ845514.1).

Salsuginus californiensis n. sp.

(Figs. 5, 6)

The following description is based on 7 specimens. With characteristics of the genus *Salsuginus* as defined by Mendoza-Franco and Vidal-Martinez (2001).

Body 426 (380-476) long by 108 (58-127) wide at midbody; haptor 53 (37-70) long by 68 (53-77) wide. Cephalic lobes with well-developed reservoirs; cephalic glands lateral to pharynx and opening anterolaterally via thin ducts. Four pigmented light receptors; anterior pair slightly smaller than posterior pair. Pharynx round in ventral view, 32 (25-39) in diameter. Mouth ventral to pharynx, with two small posterolateral lip-like swellings. Intestinal crura confluent posteriorly. Ovary ovoid, midbody; uterus and vagina thin walled; vaginal pore sinistral and at level of pharynx. Mature eggs 10 long, with small terminal knob and covered with short hairs. Testis round, posterodorsal to ovary; vas deferens passes at midbody around left intestinal crus, dilating as seminal vesicle. Penis a tapered, slightly bent tube, with an angled, sharply pointed tip; penis 20 (17-22) long (straight line, base to tip), 28 (24-34) long (along outer curve, base to tip). Accessory piece 17 (15-20) long, blunt basally, expanded at mid-length into 3 distinct ridges and 2 small teeth, and a prominent terminal hook. Dorsal and ventral anchors similar in overall shape, with long, thin, curved blade. Dorsal anchors 24 (22-25) long, length to notch 20 (17-23); superficial root 8.5 (7-11) long; deep root 4 (3-5). Dorsal bar v-shaped, 28 (24-31) in transverse length;

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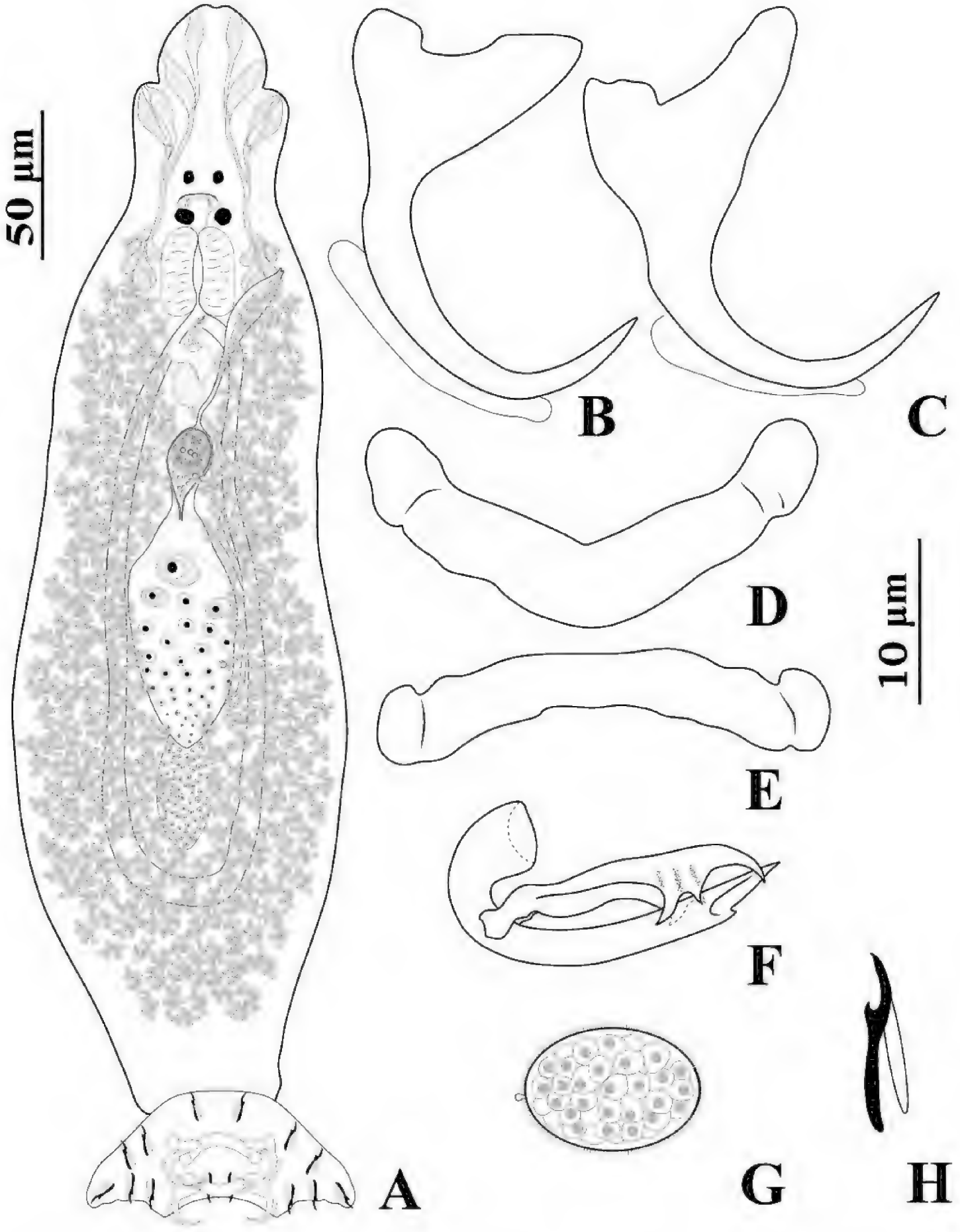

Fig. 5. Line drawings of *Salsuginus californiensis* from *Fundulus p. parvipinnis* from California. A. Body in ventral view. B. Dorsal anchor. C. Ventral anchor. D. Dorsal bar. E. Ventral bar. F. Copulatory complex. G. Egg. H. Hook.

medial width 4. Ventral anchors 23 (21-24) long, length to notch 22 (21-24); superficial root 8 (6-8) long; deep root 4.5 (4-5). Ventral bar slightly bowed, with swollen ends, 28 (27-29) in transverse length, 4 (4-5) in medial width. Larval hooks all similar in shape and size, 10.8 (10-11) long, with distinct thumb and handle that expands slightly in width along its length to a flattened upturned end.

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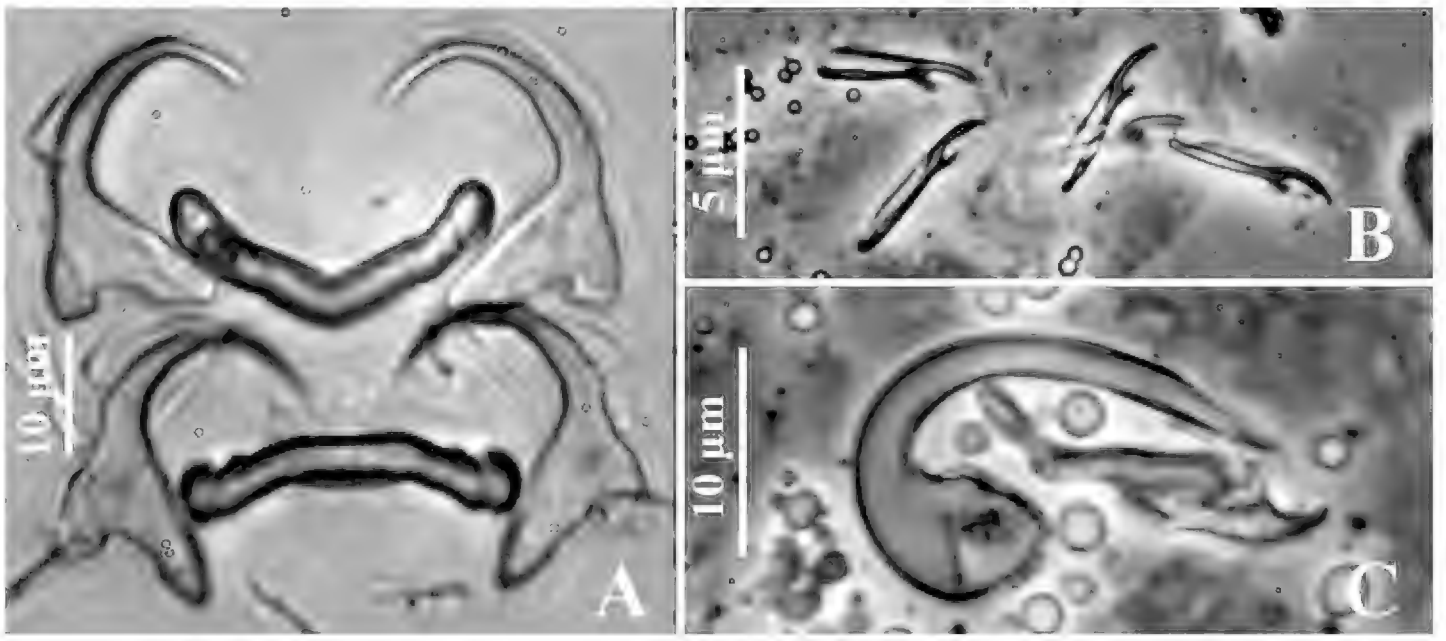

Fig. 6. Photographs of hard parts of *Salsuginus californiensis* n. sp. from *Fundulus p. parvipinnis* from California. A. Dorsal and ventral anchors and bars. B. Laval hooks. C. Male copulatory organ.

Host: Fundulus parvipinnis parvipinnis.

Type Locality: F/G Street Marsh tidal stream, San Diego Bay, CA (Table 1).

Other Localities: Salsuginus californiensis n. sp. was present on nearly all fish examined at all localities sampled (Table 1).

Site: Gill lamellae. Parasites lodged the haptor into an interlamellar space with the anchors embedded in the sides of adjacent secondary lamellae.

Type specimens: Holotype (USNM 1684307), paratype slides (USNM 1684308-1684310); paratype slide (CMA 2023.03.0004).

Molecular data: 18S rRNA gene (829 bp; Accession: OQ834412) and 28S rRNA gene (845 bp; Accession: OQ834431) have been submitted to Genbank.

Etymology: This species is named for its geographic locality.

Remarks. Salsuginus californiensis n. sp. is the 12th nominal species in the genus, the others being *S. angularis* (Mueller, 1934), *S. bahamianis*, *S. bermudae*, *S. cubensis*, *S. neotropicalis*, *S. heteroclite* Murith and Beverley-Burton, 1985, *S. thalkeni* Janovy et al., 1989, *S. seculus* (Mizelle and Arcadi, 1945), *S. spirae*, *S. umbraensis*, *S. yutanensis* Ferdig, McDowell, and Janovy, 1991. All these species have been described from fundulid and related fishes in fresh and estuarine waters of North, Central America and the Caribbean, with most species appearing specific to individual host species. Morphologically they are all very similar, with only subtle differences in anchor size and root prominences, in thickness and curvature of the penis, morphology of the larval hooks, and in ornate features of the accessory pieces (Murith and Beverley-Burton 1985).

Salsuginus californiensis n. sp. resembles *S. bahamianus*, *S. cubensis, S. neotropicalis*, *S. spirae, and S. umbraensis* in having an accessory piece that is devoid of an obvious bifurcation at the base. In each case, however, there are features that separate *S. californiensis* n. sp. from these other species. With *S. bahamianus* the penis is thinner, longer (27-34 vs 17-22 µm) and less curved, and the accessory piece has one broad tooth versus two. With *S. cubensis* the dorsal anchors are shorter (17-19 vs 22-25 µm), the penis is much narrower, and the handle of the larval hooks is needle-like in shape. In *S. neotropicalis* the larval hook handle varies in thickness along its length, and they are longer (12-14 vs 10-11 µm) than those in *S. californiensis* n. sp. In *S. spirae* the accessory piece is rod-like, less sclerotized,

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and devoid of the two prominent teeth seen in *S. californiensis* n. sp. With *S. umbraensis* the penis is thinner along its entire length compared to the more thickened and compact penis in *S. californiensis* n. sp.

The molecular data presented herein for *S. californiensis* n. sp. are the first for the genus. Searches for similar sequences in Genbank did not result in any significant matches. The sequences with the highest scores were from *Euryhaliotrematoides triangulovagina* (Yamaguti, 1968) from sunburst butterflyfish (*Chaetodon kleinii* Block, 1790) (Chaetodontidae) with a similarity of 95.5% and e-value of 0 (Accession: AY820608) for the 18S rRNA gene and *Gussevia asota* Kritsky, Thatcher and Boeger, 1989 from the oscar (*Astronotus ocellatus* Agassiz, 1831) (Cichlidae) with a similarity of 80.1% and e-value of 9e-166 (Accession: MG596661) for the 28S rRNA gene. The high level of molecular similarity between marine and freshwater ancyrocephalines, especially focusing on the parasites of butterflyfish, has been previously reported (Plaisance et al. 2005). A direct BLAST comparison of the 18S rRNA sequence data for *E. triangulovagina* (AY820608) and the freshwater *Urocleidus similis* (AJ490167.1) showed a significantly lower similarity (88.09%), implying a much closer connection between *Salsuginus* and marine ancyrocephalines. Future work collecting molecular data from marine and freshwater ancyrocephalines will likely provide insight into these interesting relationships.

Discussion

The monogeneans reported herein from the California killifish are all new records for the Pacific coast of North America. There are several reports of species of *Gyrodactylus* and *Salsuginus* from *F. lima,* Oaxaca killifish (*Profundulus punctatus* (Günther, 1866)), *Profundulus oaxacae* (Meek, 1902) and guppy (*Poecilia reticulata* Peters, 1859) (all cyprinodontoids) inhabiting freshwaters throughout Mexico, including the Pacific coastal drainages (Martinez-Aquino et al. 2004, Méndez et al. 2010; Pinacho-Pinacho et al. 2014; Garcia-Vásques et al. 2018; Salgado-Maldonado et al. 2020). This monogenean community is like that reported from related host fundulids east of the Rocky Mountains in being comprised of species of *Gyrodactylus, Fundulotrema* and *Salsuginus.* One species, *F. prolongis,* is listed from fundulid hosts from Colorado to the Great Lakes and Florida to Nova Scotia (Hoffman 1999). King and Cone (2009) reported *G. stephanus, F. foxi, F. porterensis*, and *F. prolongis* from *Fundulus diaphanus, Fundulus heteroclitus*, and hybrids between the latter two host species, all living in a coastal brackish water lake in Nova Scotia. The Californian monogenean community is unique from its eastern counterpart by having two common species of *Gyrodactylus* on a single host species. All four species reported herein were encountered on the same fish at the F/G Street site in San Diego Bay (Table 1). In the east, hosts are reported to have only single species infections, either *G. bulbacanthus* Mayes, 1970, *G. funduli* Hargis, 1955, *G. stephanus* Mueller, 1937 or *G. stegurus* Mueller, 1937. Available genetic data (King and Cone 2009) shows the latter species is not closely related to either *G. parvipinni* n. sp. or *G. kalmanae* n. sp., which suggests that separate origins and/or isolation has occurred among the *Gyrodactylus* that infect fundulid hosts.

Fundulus lima and the two subspecies of *F. parvipinni* form an unresolved trichotomy that diverged 300,000 to 400,000 years ago (Bernardi et al. 2007) and today are isolated from congeners found in fresh and coastal waters east of the Rocky Mountains. Twenty million years ago, ocean covered what is presently the Isthmus of Panama and waters flowed freely between the Pacific and the Atlantic (Molnar 2008). As a result of plate tectonics and uplifting, islands started forming and by 3 to 3.5 mya the Isthmus of Panama was

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formed and flow of ocean water between the Pacific and Caribbean halted (Molnar 2008). Given the widespread distribution of *Salsuginus* on fundulid fishes throughout the continent (Hathaway and Herlevich 1973; Cloutman 1974; Murith and Beverley-Burton 1984; McAllister et al. 2019a, b) and coastal waters (Murith and Beverley-Burton 1984; Hoffman 1999), ancestral *Salsuginus* appear to have parasitized fundulids early in the rapid, repeated radiation of these fishes deep into the freshwaters of the continent and along the entire temperate and tropical coasts of North America (Whitehead 2010). Some fishes which tolerate salinity fluxes are known to pass through the freshwaters of the Panama Canal between the Pacific Ocean and Caribbean (Hildebrand 1939) but whether this has historically involved fundulids is not known. The presence of *Salsuginus* on fundulids and poeciliids endemic to the Pacific drainage and coast further suggests the ancestral parasite was isolated from eastern congeners by the formation of the Isthmus of Panama. Moreover, molecular analysis involving *G. parvipinni* n. sp. and *G. kalmanae* n. sp. suggests that these parasites were acquired prior to Pacific isolation as the genetic distance of these parasites from other known *Gyrodactylus* spp. combined with the distinct genetic lineage associated with *F. parvipinnis* (Whitehead 2010) supports that these fish and parasites may have coexisted for an exceptional period of time in isolation.

The finding of *F. prolongis* with partial 18S and ITS sequences essentially identical to eastern populations raises questions about its occurrence in California. The millions of years of geologic separation since the formation of the Isthmus in Panama is a time scale sufficient for allopatric speciation to occur and slightly larger than the time scale calculated (1.64 to 2.48 Mya) to produce the extant species within the *Gyrodactylus wageneri* group (Leis et al. 2021). This extended period of isolation would also appear to explain the aforementioned genetic distances associated with *G. parvipinni* n. sp. and *G. kalmanae* n. sp. and also suggest that *F. prolongis* was acquired in the recent past. A reasonable explanation is that *F. prolongis* could have entered Californian coastal waters via introduction of infected fundulids from eastern North America. As mentioned above, this parasite has been reported from a variety of host species of *Fundulus* and related *Cyprinodon* throughout central and eastern North America and appears to have broad specificity within cyprinodontiform fishes of the continent. Several species of fundulid killifish (*L. parva* in San Francisco Bay and estuary, Irvine Lake and Goleta Point Lake; and *L. goodi* in the San Dieguito River and the Sacramento-San Joaquin Delta) endemic to eastern North America are known to have established populations in fresh and coastal waters of California (Hubbs and Miller 1965; Fuller et al. 1999; Huang et al. 2003; Mahardja et al. 2016; O'Rear et al. 2020; Fuller and Neilson 2022; Fuller 2022) and could have been the source of *F. prolongis*. If *F. prolongis* has in fact been introduced into California it should be considered a non-native species.

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Wind-Event-Induced Ocean Upwelling, Relaxation and Chlorophyll Response in the Southern California Bight

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Abstract.—The consequences of a large wind event occurring in the Southern California Bight on 31 January 2016, are analyzed using data from nearshore island and mainland seabed thermographs (10 to 20 m depths), NOAA meteorologic and wave-rider buoys, a CalCOFI cruise and SST and Chl a data products from satellite remote sensing. Discernible upwelling was discovered approximately 7 hr after the northwesterly wind surpassed 10 m/s, and ultimately coastal water shoaled by at least 90 m. The upwelling character varied according to where the measurements were taken. Leeward seabed thermographs and near mainland shore buoys registered an impulse-like temperature decrease, whereas open-ocean and windward sites measured a more gradual change. The approximately one day long event was followed by an increase in Chl a throughout the bight, with the largest increase being adjacent to the mainland. The Chl a signal vanished after about one week and the temperatures returned to pre-event levels after 11 d. Various upwelling and temperature-relaxation mechanisms are discussed, with two separate upwelling mechanisms suggested and the most likely candidate for relaxation being lateral diffusion of warm offshore water into the nearshore upwelled water.

Wind-induced upwelling in the Southern California Bight (SCB) is notably different from the widespread upwelling along the Northern and Central California coasts. The latter is produced by seasonal alongshore winds and Ekman transport and pumping (Pringle and Dever 2009). These alongshore winds do not extend to the SCB coastline due to the different coastline orientation of the bight and its surrounding mountains. Modeling by Jacox et al. (2014), indicates that Central-California-like upwelling is much reduced south and east of the Northern Channel Islands. However, episodic offshore-wind events (e.g., Santa Ana winds and some storms) do produce upwelling in the bight. These winds are anecdotally noted by beach divers to produce excellent diving conditions with unusual cross-shore currents, resulting in clear though cold water off the beach, and small-surf entry due to opposing-wind mitigation of incoming swells. As offshore SCB winds often occur when the bight is relatively nutrient impoverished, that is, in the fall and beginning of winter, they may be significant to the nutrient supply during these seasons. Indeed, Santa Ana winds have been associated with phytoplankton blooms offshore southern California (Hu and Liu 2003; Trasvina et al. 2003). Toward determining this significance, I wish to understand the phenomenology of local wind-induced upwelling and its relaxation.

I chose a case study corresponding to an intense offshore wind event that was measured by the David Tsao Continental Thermograph Array (DTCTA). In addition to this array, a number of independent programs recorded and archived data pertaining to the event. These include the Channel Islands National Park (CINP) Kelp Forest Monitoring program, the National Data Buoy Center (NDBC), California Cooperative Oceanic and Fisheries Investigation (CalCOFI), as well as the Earth Observation System (EOS) satellite

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Table 1. DTCTA Sites.

Name and map designation	Lat °; Long °	Depth m
Deer Creek (DT0)	34.060; −118.989	9.1
Marine Land Platform (DT1)	33.736; −118.391	17.1
White Point Rock (DT2)	33.714; −118.319	20.4
Deadman (DT3)	33.546; −117.802	9.1
Deadman (DT4)	33.546; −117.802	18.3

program. The issues to address include: 1) quantification of the upwelling (i.e., the amount of water and nutrients upwelled) and how far into the bight are upwelling effects found; 2) the upwelling time scale and mechanisms; 3) the upwelling-relaxation time scale and mechanisms; and, 4) quantification of the biological response to the upwelling. The size of the chosen event is probably not typical of wind-induced upwelling, but its large signal enables easier detection of the event's phenomena and understanding of the physical processes involved. Although similar upwelling in the SCB has been studied in the past (Dong et al. 2011), the present analysis is distinguished by the large number of *in situ* observations, especially those at depth, coupled with biological data.

In the sections that follow, I describe the datasets and the event, including relevant time scales. Then I proceed to quantify the character and amount of upwelling. Next, I discuss upwelling and relaxation mechanisms as well as the biological response within the context of previous studies. I describe how the physical mechanism can influence the biological response and end with a brief conclusion.

Materials and Methods

Our source materials include datasets from measurements made with coastal seabed thermographs, meteorological buoys, Coastal Marine Automated Network (C-MAN) and water-level stations, a CalCOFI cruise and satellite remote sensing products. Temperature was collected on the seabed just off the coast with the DTCTA, which is a volunteer effort to monitor ocean temperatures immediately adjacent to the Los Angeles metropolitan area. The locations and depths of the five Onset thermographs (part number U22-001) used in DTCTA are listed in Table 1. Their uncertainty is ~0.1 °C, sampling period was 30 min, and timing drift estimated to be less than 2 min during their deployment; however, there is a 1 hr uncertainty in the time stamp produced by ambiguity between standard and daylight savings time regarding initial programming of the devices. These uncertainties and errors are insignificant when compared to the temporal scales and temperature changes measured. These sensors span a large section of the bight with the shortest distance from the northern-most sensor at Deer Creek to the southernmost sensors at Deadman Reef in Laguna Beach, CA being 123 km and with the along-coast distance being much longer. There are two sensors at different depths at Deadman Reef, enabling water-column gradient measurements there.

A similarly instrumented thermograph array with the same uncertainties and 1 hr sampling is maintained by the Channel Islands National Park (CINP), as part of their kelp forest monitoring program. The sites from which temperature data were used are listed in Table 2. These sites are typically at about 12 m depth and located mostly on the Northern Channel Islands, characterized as being ~40 km from the mainland, although two sites

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Table 2. CINP Sites.

Site name (map designation)	Lat °; Long °	Depth (m)
Hare Rock (CW0)	34.06, −120.35	6.2
Rodes Reef (CW1)	34.03, −120.10	13.6
Frys Harbor (CW2)	34.05, −119.75	12.4
Pelican Bay (CW3)	34.03, −119.70	6.5
Cavern Point (CW4)	34.05, −119.56	12.2
Keyhole (CW5)	34.01, −119.43	9.0
Cathedral (CW6)	34.01, −119.37	8.1
Wyckoff Ledge (CL0)	34.02, −120.38	13.2
Johnson's Lee North (CL1)	33.90, −120.10	10.1
Cluster Point (CL2)	33.92, −120.18	13.8
Gull Island South (CL3)	33.94, −119.82	15.8
Yellow Banks (CL4)	33.98, −119.56	15.4
Admiral's Reef (CL5)	34.00, −119.43	13.5
East Fish Camp (CL6)	34.00, −119.38	11.6
Arch Point (CL7)	33.48, −119.02	7.6
Sea Lion Rookery (CL8)	33.46, −119.02	13.1

are located on the eastern side of Santa Barbara Island in the southern group of Channel Islands.

Buoys include the classic National Oceanic and Atmospheric Administration (NOAA) meteorological buoys that provide significant wave height (SWH), water and air temperatures, wind speed and direction; and, wave-rider buoys which provide water temperature and wave height. Buoy water temperature measurements are made approximately 0.5 m beneath the surface. These datasets were retrieved from the NDBC archive (www.ndbc.noa.gov). C-MAN and water-level stations' data retrieved from the same archive provided wave height, water temperature or wind/air data with a sampling period of ≤1 hr. The sensor platforms are listed in Table 3, with their location, depth of water, and data types among water temperature (WTMP), wave height (WVHT), wind speed (WSPD), wind direction (WDIR) and air temperature (ATMP) available for the event. Again, uncertainties in the NOAA archived measurements are much smaller than the natural variations I wish to examine. All sensor dates are converted to UTC and times series are plotted versus hour of year 2016. With the exception of station ICAC1, occasional single-measurement dropouts in data were replaced with the average of the two adjacent data points, with such repairs being performed on fewer than 10 measurements. ICAC1 data had many dropouts during the period of interest and were not used in numerical calculations, though its good data were inspected to ensure consistency with the other data sets.

A map illustrating the locations of the platforms (Fig. 1). The site designations on the map are particular to this study for conciseness and are keyed to institutional designations in the tables. DTx is the DTCTA site number x, MBx is the meteorological buoy site x, WRx is the wave-rider x site, etc. For later analysis, I separate in symbology the leeward and windward CINP thermograph locations, CLx and CWx, respectively. C-MAN and water-level stations are designated as nearshore, or NSx. From the map can be seen that the NOAA datasets are sited such as to surround the DTCTA locations and the CINP sites are farthest from the mainland in the bight.

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Table 3. NDBC Stations.

Buoy (map designation)	Lat °; Long °	Bottom depth (m)	WTMP	WVHT	WSPD	WDIR	ATMP
46054 (MB0)	34.273; −120.470	454	y	y	y	y	y
46053 (MB1)	34.241; −119.839	405	y	y	y	y	y
46025 (MB2)	33.758, −119.044	890	y	y	y	y	y
46251 (WR0)	33.769; −119.565	1890	y	y			
46221 (WR1)	33.860, −118.641	387	y	y			
46222 (WR2)	33.618, −118.317	483	y	y			
46256 (WR3)	33.700; −118.201	23	y	y			
46253 (WR4)	33.576; −118.181	66	y	y			
46223 (WR5)	33.458; −117.767	370	y	y			
46258 (WR6)	32.752; −117.501	562	y	y			
46224 (WR7)	33.178; −117.472	238	y	y			
46242 (WR8)	33.220; −117.439	20	y	y			
46232 (WR9)	32.517, −117.425	1049	y	y			
46225 (WR10)	32.933; −117.391	572	y	y			
46254 (WR11)	32.868; −117.267	46	y	y			
PTGC1 (NS0)	34.577; −120.648	NA			y	y	y
NTBC1 (NS1)	34.405; −119.692	NA			y	y	y
ICAC1 (NS2)	34.008, −118.500	10.3 *	y		y	y	y
OHBC1 (NS3)	33.720, −118.273	2.1 *	y				
LJPC1 (NS4)	32.867; −117.257	6.6		y			

* Depth of temperature measurement.

Other datasets include those from the 2016 winter CalCOFI cruise and products from the Ocean Biology Processing Group of the National Air and Space Administration (NASA) Color Group (oceancolor.gfsc.nasa.gov). The CalCOFI measurements, though acquired before the upwelling event analyzed, are used to estimate water-column parame-

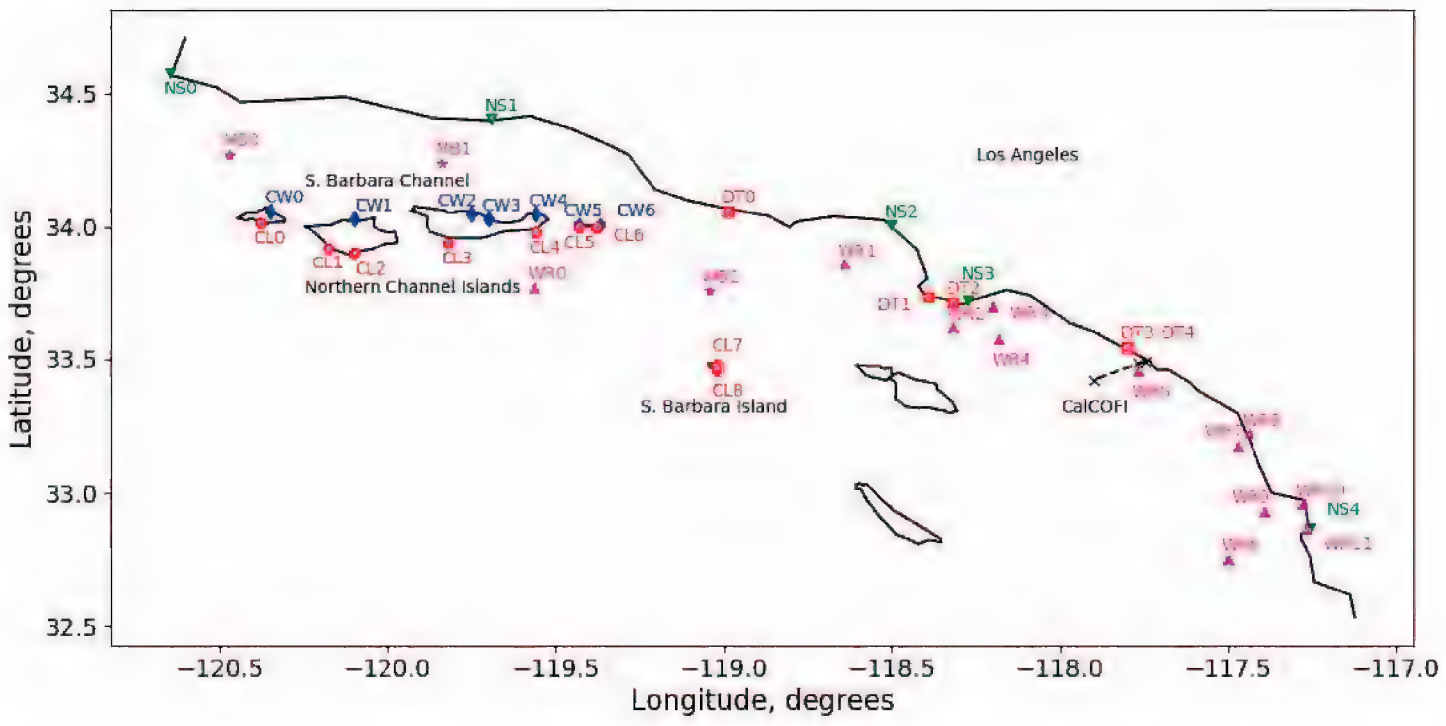

Fig. 1. Location of data sites keyed to Tables 1 – 3. MB is meteorological buoy, NS is nearshore station, WR is wave-rider buoy, DT is DTCTA site, and CW and CL are CINP-windward and CINP-leeward sites, respectively.

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ters and data types that are not sampled by the other assets. The section of the cruise from which data are displayed is shown on the map. The stations closest to the DTCTA Laguna thermographs (DT3 and DT4) were sampled on 13 January 2016, (i.e., 18 d before the event) providing measurements of the water column 8 - 53 km from the thermographs. The CalCOFI station IDs are (90.0, 027.2) (90.0, 028.0), (90.0, 030.0) and (90.0 035.0). The farthest stations (90.0, 030.0; 90.0 035.0) were used as the seabed depth there surpassed the thermocline depth, enabling its identification. Remote sensing products include sea surface temperature (SST) and chlorophyll-a (Chl a) from the MODIS instrument on the Aqua (EOS PM) satellite. These 8 d, 4 km geo-registered (i.e., standard mapped imagery) samples are obtainable over a widespread area (almost globally), though at a much slower sampling rate than the *in situ* sensors.

My analysis methods include inspection of time series to identify and quantify changes and extracting and averaging of data from derived imagery to form time series. To quantify (upwelling) temperature change characteristics, I fit a sigmoid-like function to the temperature data for each station from hr 715 to 800 of year 2016. The function is

$$T(t) = a\frac{-e^{b(t-t_0)} + e^{-b(t-t_0)}}{e^{b(t-t_0)} + e^{-b(t-t_0)}} + T_0 \qquad \text{Eq. 1}$$

Here, t is time and T is temperature. The parameters a, b, t_0 and T_0 represent the amplitude (one-half the total temperature change), the time scale of change, the phase (time when the temperature has changed by ½ the total change), and the temperature (offset) at that time, respectively. Immediately derivable is the model temperature slope at t_0:

$$\left.\frac{\partial T}{\partial t}\right|_{t_0} = -ab$$

which I term the upwelling temporal gradient, which can be either positive or negative. I can also estimate a commencement time, t_c, from the extracted parameters. I define this time to be

$$t_c = t_0 + \frac{1}{2b} ln\left(\frac{1-\beta}{1+\beta}\right)$$

where $(1 - \beta)/2$ is the fractional change in temperature relative to total change defining event commencement. For this study, I define t_c as the time the temperature decreases 2.5% of the total change, i.e., $\beta = 0.95$. These extracted quantities characterize the upwelling event during its commencement at each station.

I use water-column profiles to quantify upwelling by assuming the upwelling temporal gradient is produced by vertical advection of the depth gradient. Downwelling or relaxation temporal gradients are determined by inspection or by a simple linear fit to the data from its event temperature minimum to its recovery. Time series of Chl a and SST responses are produced by averaging small spatial regions of remotely-sensed values from the temporal samples received from the archive.

Results

A large upwelling event occurred on 31 January 2016 when there was a sharp decrease of >2 °C at all five DTCTA thermographs beginning at hr 744. To place it within context, DTCTA data from 1 December 2015 to 31 March 2016 are shown in the top panel of Fig. 2. Seasonally, the temperature in the inner bight will be a minimum in March (Gelpi and Norris 2008), and there is a downward trend in temperature over the interval plotted,

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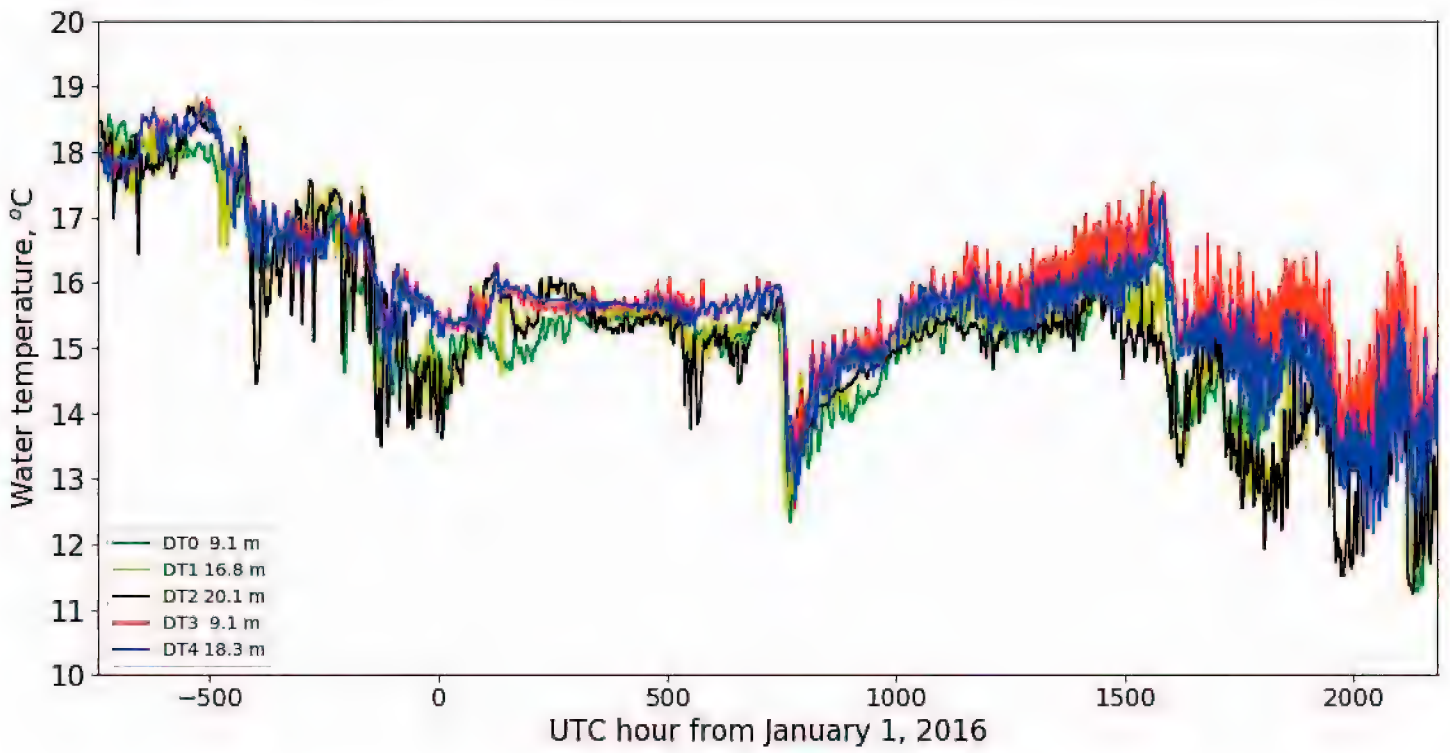

Fig. 2. Temperature from DTCTA sites.

as expected. Although upwelling events are commonplace in DTCTA data from individual sites (notice the temperature drop at DT2 around hr 500; Fig. 2), the large amplitude and widespread occurrence of the January 31 event identified this event for study.

The event occurred when there was little stratification as evidenced by the dearth of internal waves and also similar temperatures at the two depths at Deadman Reef (DT3 and DT4). There is little lateral gradient as the disparate sites have similar temperatures. The event is shown on an expanded time scale in the top panel of Fig. 3. It is exemplified by DT0 data, where the temperature started to decrease at hr 744 when it was 15.61 °C and ended at hr 767 with the temperature at 12.34 °C. That is, in less than 24 hr, the temperature dropped 3.3 °C. The temperature recovered to its pre-event value at hr 1035, or 268 hr (or 11.1 d) later. After the initial impulsive temperature drop, the water temperature increased approximately linearly with time.

The wind measurements from three reporting nearshore stations are shown (Fig. 4). For the event, wind speed peaked at 25 m/s at Pt. Conception (NS0), was out of the north/north west and brought cooler air. This also coincides with the measurements made at the meteorological buoys (MB0, MB1 and MB2) located offshore, shown in the top two panels of Fig. 5. The meteorological buoys also measured a drop in air temperature (not shown), a large increase in wind speed (top panel of Fig. 5), and wind out of the north and northwest (middle panel) providing a cross-shore component to the wind vector. The meteorological buoy wind measurements indicate the wind speed surpassed 10 m/s at hr 735 and reduced to below 10 m/s at hr 767. Defining the wind event using a 10 m/s threshold, its duration was approximately 32 hr.

Meteorological buoy water temperatures, shown in the bottom panel of Fig. 5, indicate that the water temperature offshore began a slow decline of about 1 °C beginning at the start of the wind event, and lasting till ~hr 815. At the wave-rider buoys, lower water temperatures were noted as coincident with the start of the event (Fig. 6), with the exception of the wave-rider buoys I designate as WR0 and WR6. These buoys were located much farther from shore when compared to the location of the other wave-rider buoys (Fig. 1). A decrease in water temperature was also found along the Northern Channel Islands. The

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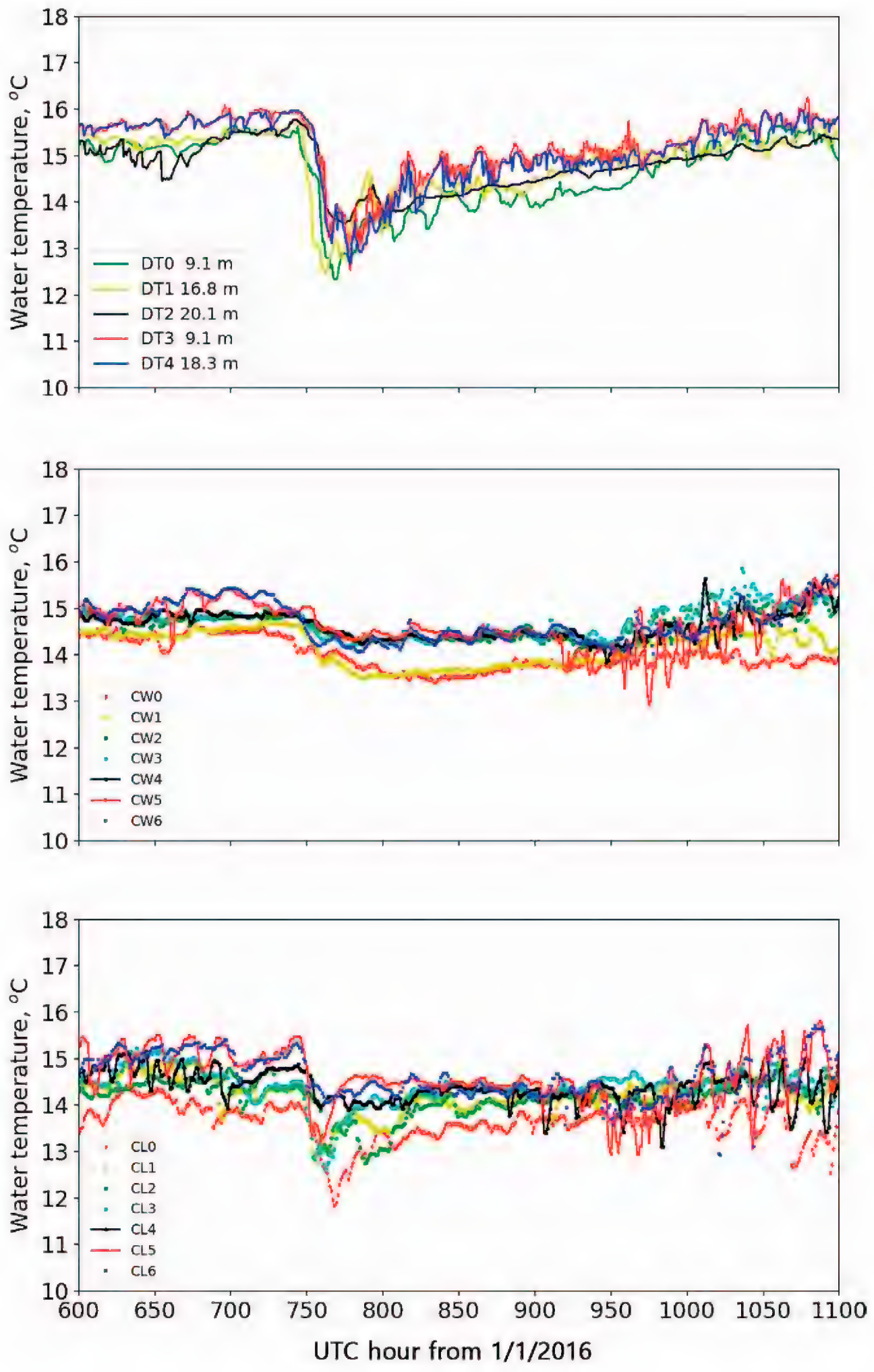

Fig. 3. Expanded view of DTCTA and CINP temperature data.

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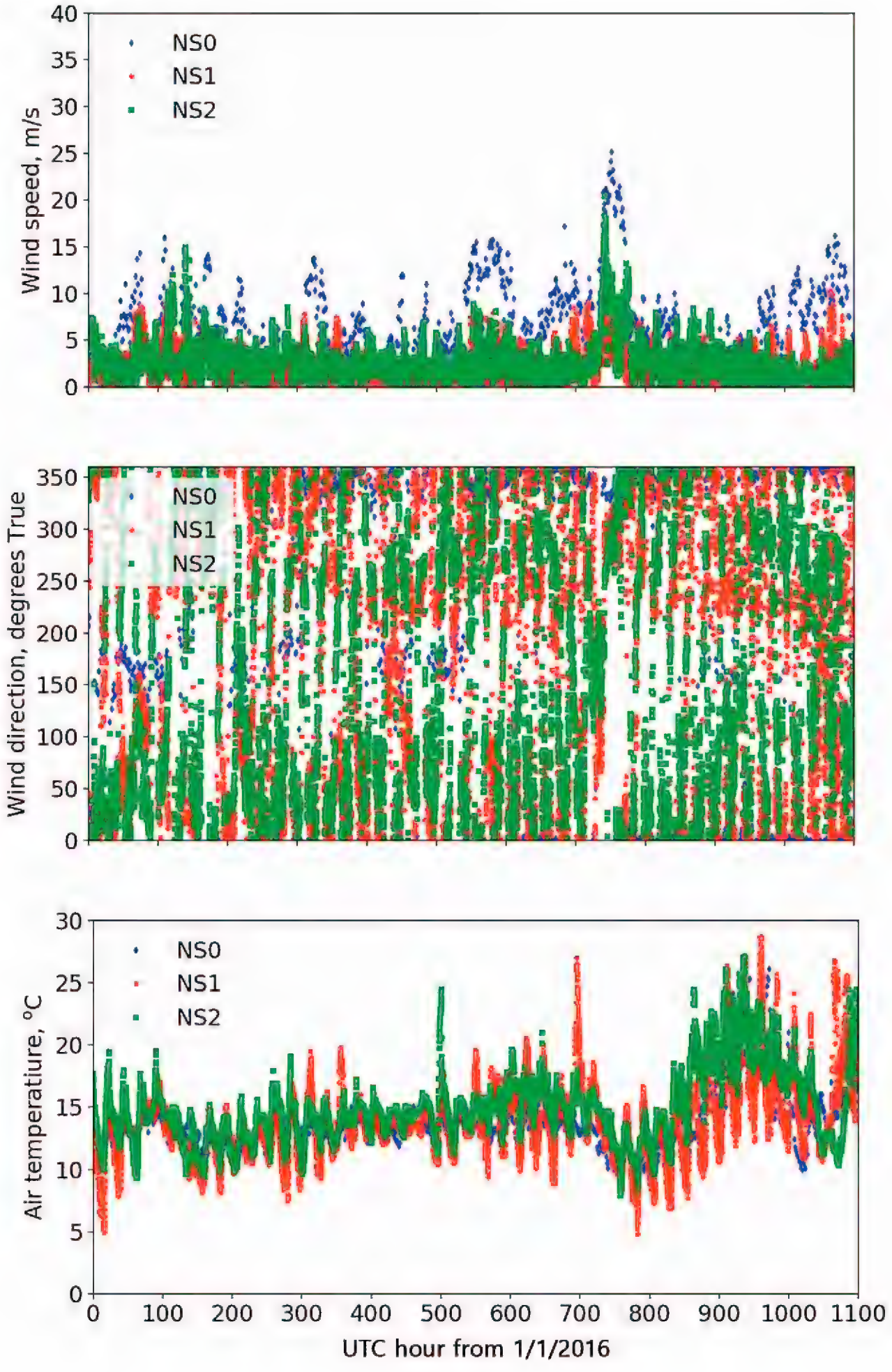

Fig. 4. Wind speed (top), direction (middle) and air temperature (bottom) from nearshore sites.

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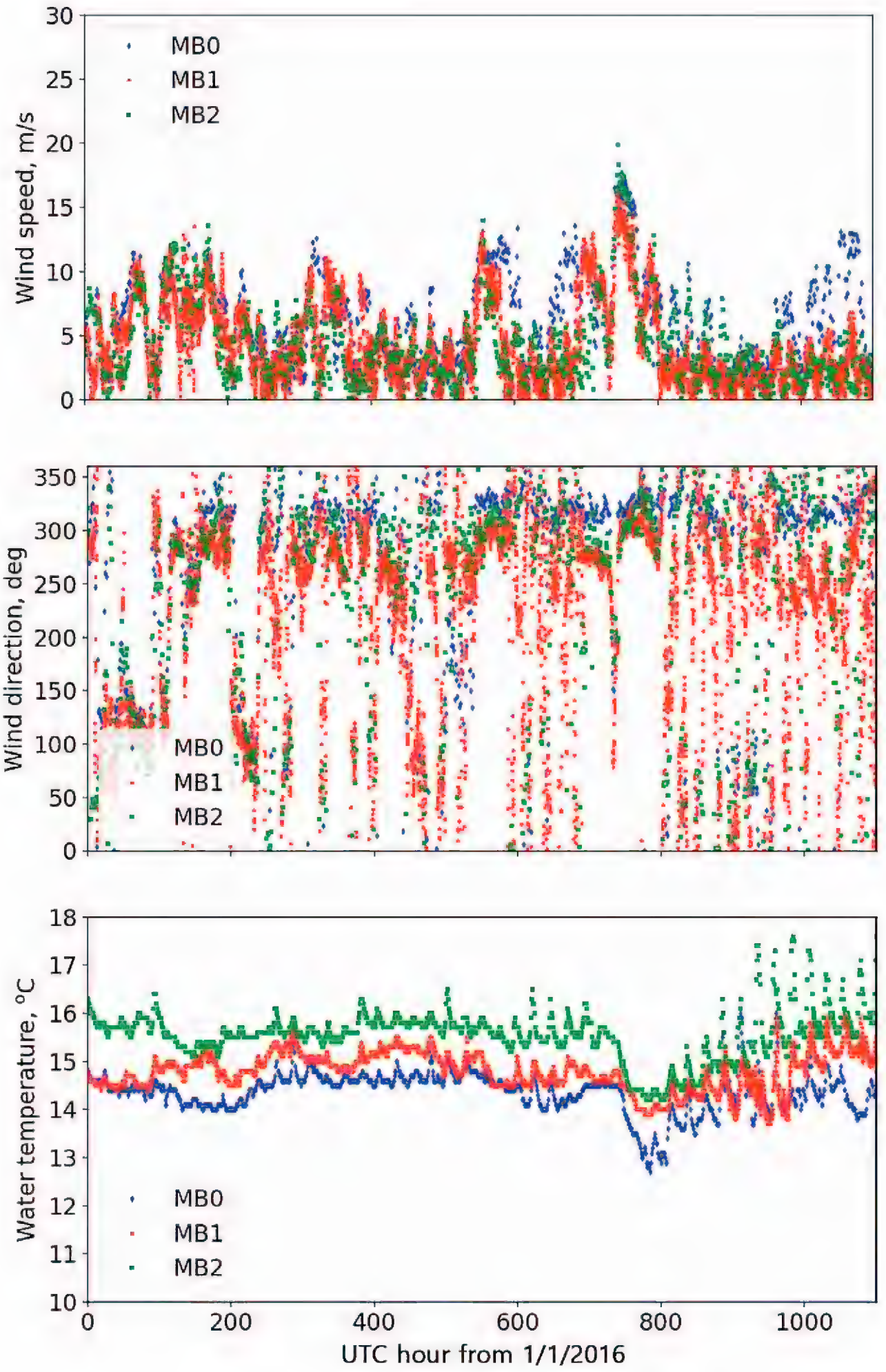

Fig. 5. NOAA meteorological buoy data, wind speed (top), direction (middle) and water temperature (bottom).

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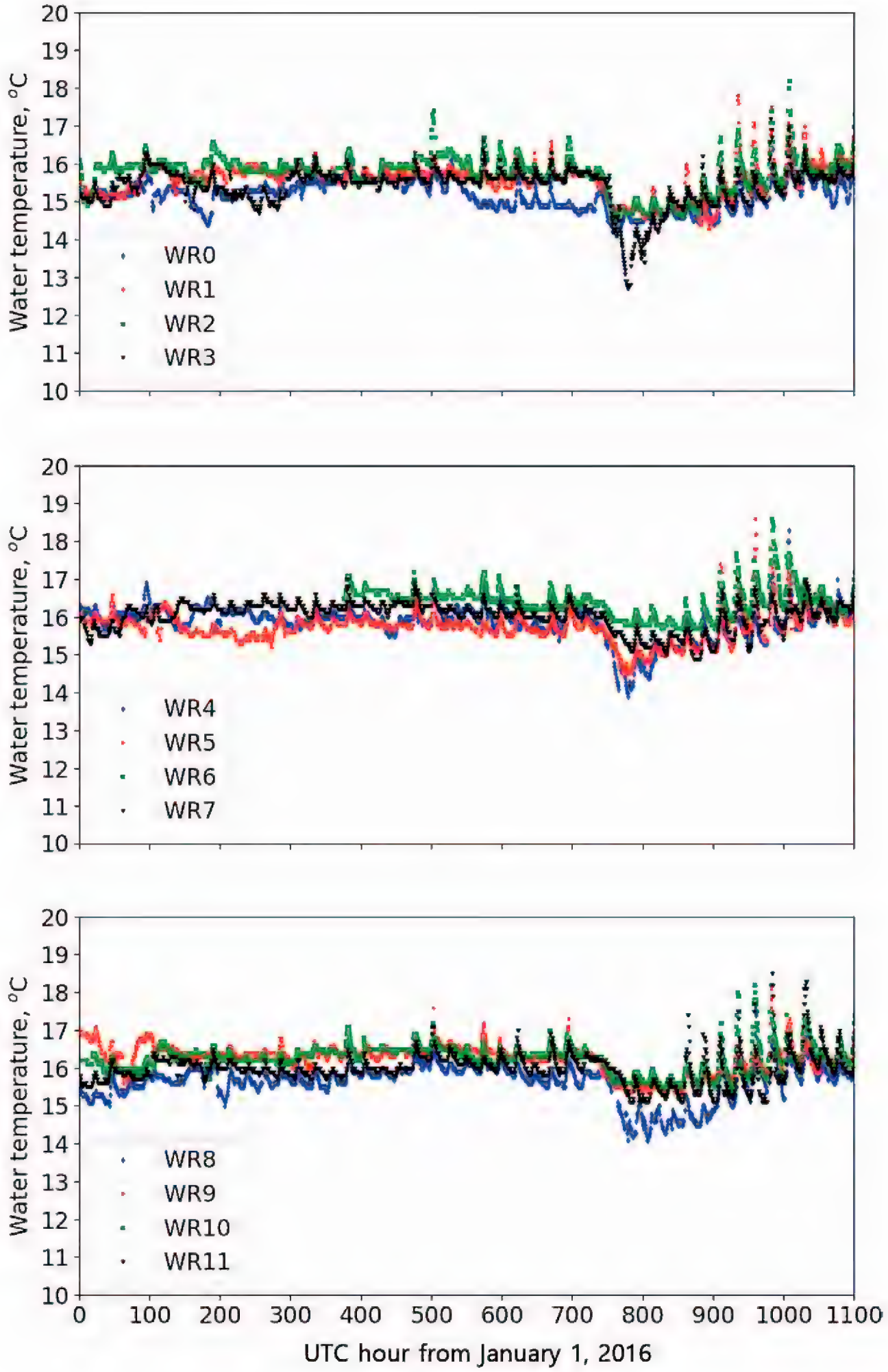

Fig. 6. Water temperature from wave-rider buoys, designated by map nomenclature.

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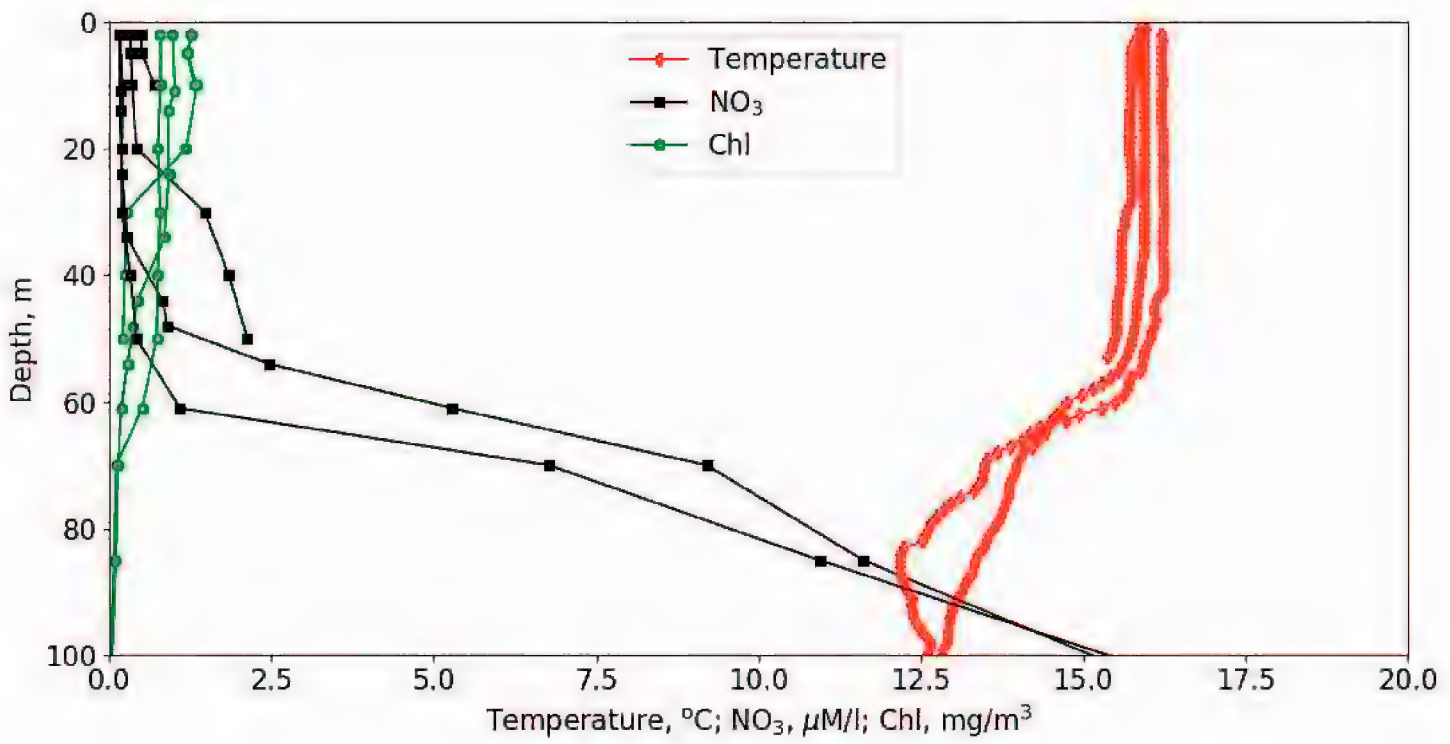

Fig. 7. Four CalCOFI water profiles from 13 January 2016, along the line shown in Fig. 1. Deepest sampled depth and near-surface temperature decrease toward the coast, near-surface nitrate and chlorophyll increase toward the coast. Station locations are given in the text.

CINP data are shown (Fig. 3) for easy comparison to the DTCTA data. The CINP data are divided into the windward side (for this event) shown in the middle panel, and the leeward side in the bottom panel. In both plots the expected lateral gradient is evident (colder temperatures farther west) and there is a reduction in temperature at all sites beginning at near hr 743 or so; however, the character of the reduction is different between the two sides, the leeward side having a larger and faster reduction in temperature as compared to the windward side. The leeward CINP sites experienced a temperature decrease that was similar to those measured by the leeward DTCTA, here described as an impulse. However, the windward instruments measured a gradual decline in temperature, though they were between the leeward island and mainland sites. The CINP sensors on Santa Barbara Island are also located on the leeward (east) side of the island and their data also exhibit an impulsive change (not shown).

The CalCOFI profiles are used to estimate the nominal depth from which the upwelling water originated, which in turn, enables inference of the nutrients amounts provided by the upwelling, importantly nitrate (Palacios et al. 2013). The four temperature, nitrate and chlorophyll profiles are shown (Fig. 7). The upper-water column was well mixed with the mixed-layer-depth extended to 58 m, and with a large temperature gradient found between 58 and 62 m. Correlated with this decrease in temperature was a large increase in nitrate. The chlorophyll data indicate that there was no Deep Chlorophyl Maximum depth.

Chl a and SST data products were examined for evidence of the consequences of the upwelling event. Two samples of the Southern California Bight are shown as a map (Fig. 8), with the first sample representing 25 Jan – 1 Feb and the second sample corresponding to 2 Feb – 9 Feb, the week after the event. For the latter data, there is a significant increase in chlorophyll relative to the former throughout the bight but especially both in the Santa Barbara Channel and along the coast of the Los Angeles metropolitan region. Additionally, on the map are regions represented by boxes along Los Angeles denoting the

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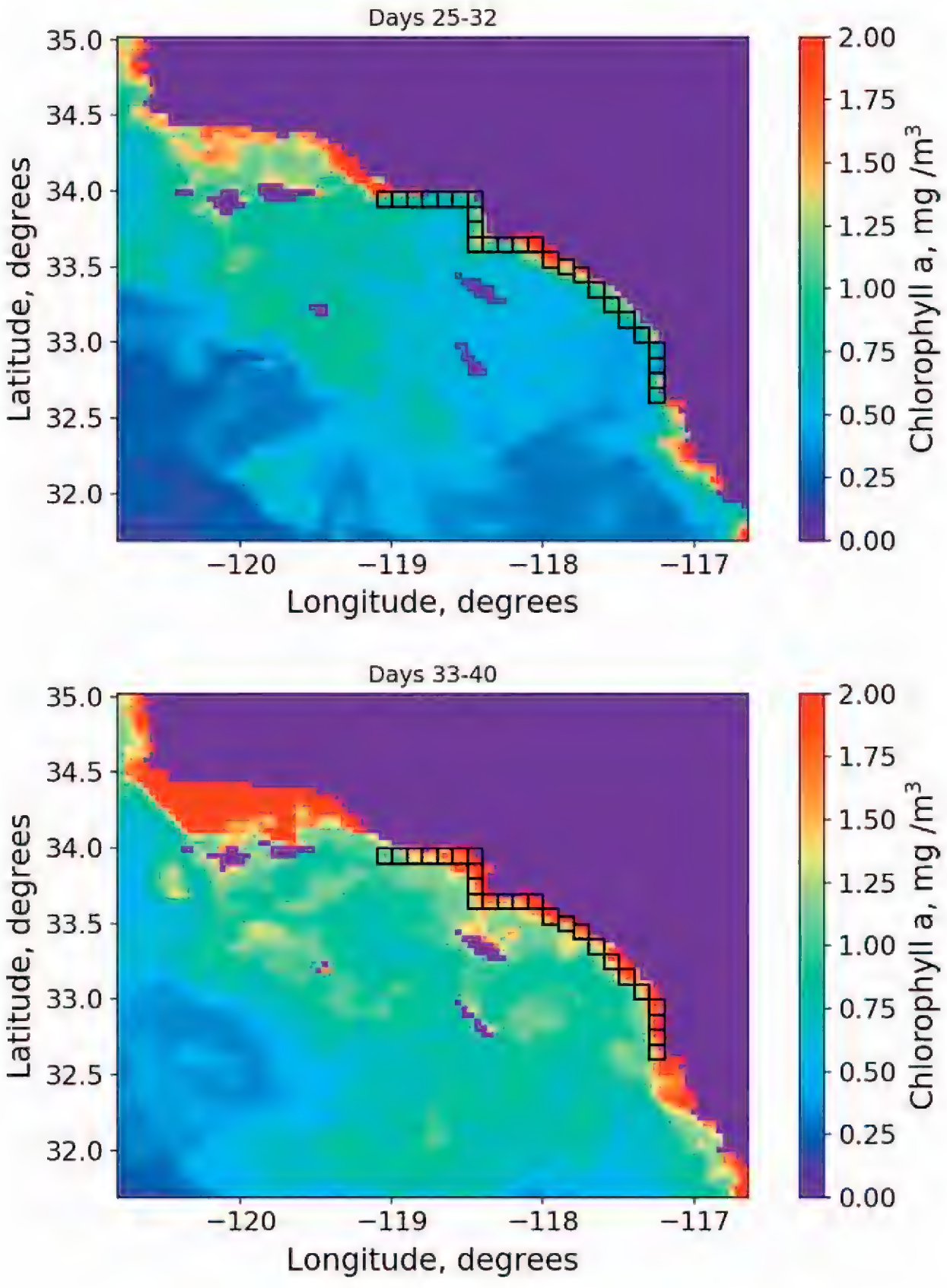

Fig. 8. Map of remotely-sensed chlorophyll-a values for d 25-32 (top) and 33-40 (bottom).

area used to compute an average nearshore Chl a value. The boxes are $0.1^{\circ} \times 0.1^{\circ}$ square or approximately 100 km^2, each. The average Chl a value among the pixels in each box was computed. The mean value among the boxes plus and minus the standard deviation among the boxes are shown as a function of sampling interval (top panel Fig. 9). There can be much natural variation along the coast and this can be represented by the variance among the box averages. The standard deviation is not an uncertainty, but is related to the coherence among the boxes. The data indicate that there was a significant chlorophyll response (~100% increase to 1.4 mg/m^3) after the upwelling event and it vanishes two weeks

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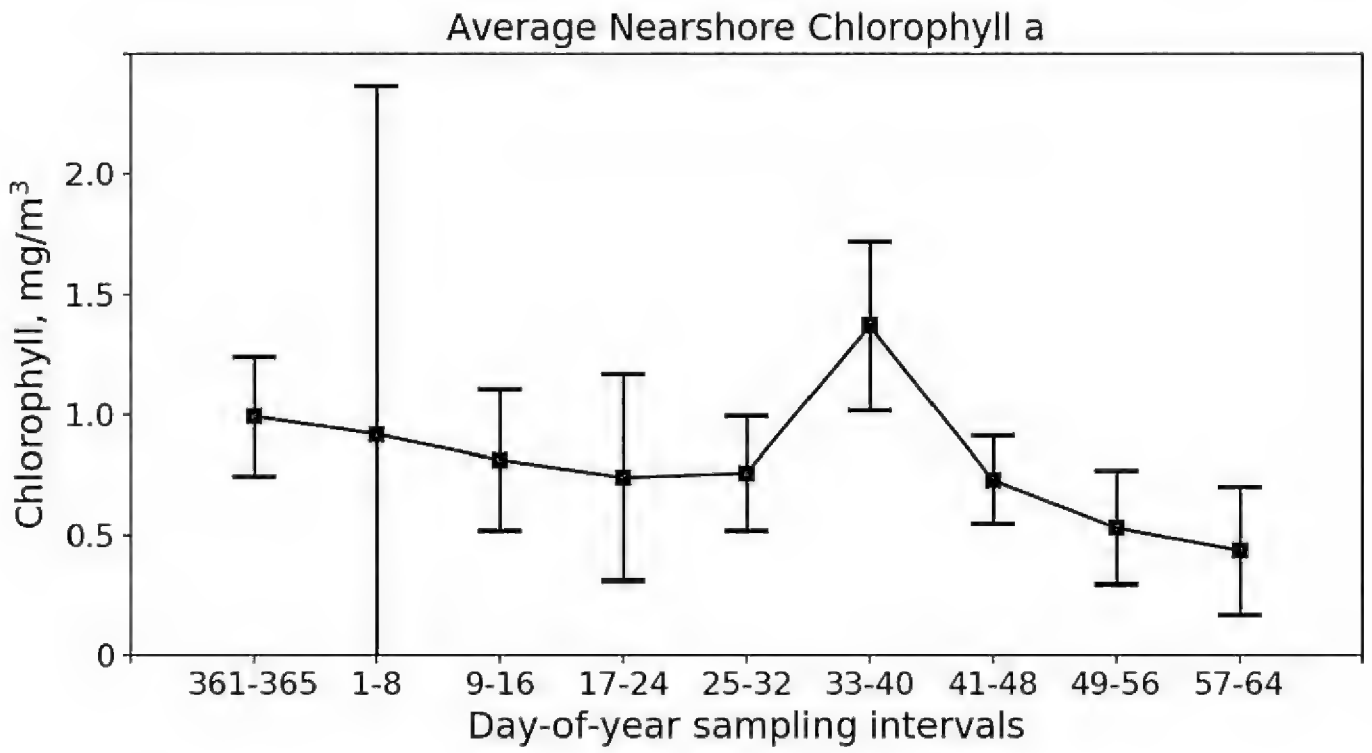

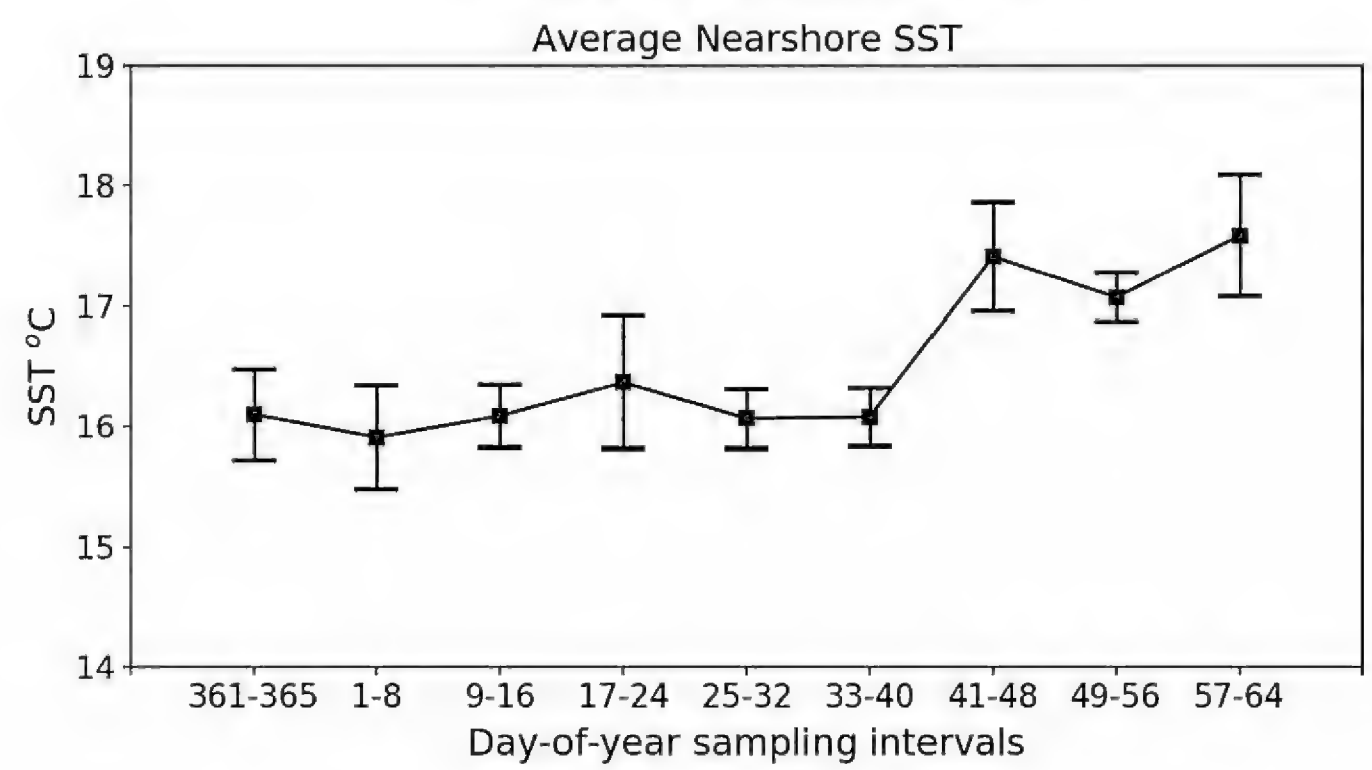

Fig. 9. Time series of nearshore average values among the areas denoted by the boxes in Fig. 8. Top Panel: Chl a, bottom panel: SST.

after the event. Also, the signal is not produced by a small number of boxes with large values.

The SST response, computed in a similar manner, is shown in the bottom panel of Fig. 9, and is not striking. The average SST value is much higher than the at-depth measurements made by the DTCTA, which could be the difference between the ocean skin temperature and water column. The signal may represent a significant reduction in the apparent seasonal climb in SST, from 16 °C for d 1-8 to 17.5 °C for d 57-64. With this interpretation, the event's signal magnitude is ~0.75 °C, i.e., SST decreased by ~0.75 °C during the upwelling.

Equation 1 was fitted to 36 data sets with water temperature data. Two sites, NS2 and NS3, were not fitted due to the number of bad data points (NS2) or location within the Los Angeles Harbor complex (NS3), where data may not be representative of ocean values.

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Table 4. Retrieved Fit Parameters.

Site	Amp (°C)	Scale (hr^{-1})	Phase (hr)	Offset (°C)	Gradient (°C hr^{-1})	Ln (-grad)	t_c, (hr)
DT0	1.17	0.18	755.7	14.3	−0.21	−1.56	745.6
DT1	1.06	0.42	750.7	14.5	−0.45	−0.79	746.3
DT2	0.85	0.34	758.6	14.7	−0.29	−1.23	753.1
DT3	1.18	0.17	758.6	14.7	−0.2	−1.6	747.6
DT4	1.28	0.2	758.4	14.6	−0.26	−1.34	749.1
WR0	0.26	0.53	748	14.7	−0.14	−1.96	744.5
WR1	0.48	0.09	743.9	15.3	−0.04	−3.21	722.4
WR2	0.49	0.22	748.9	15.3	−0.11	−2.2	740.5
WR3	1.07	0.09	757.5	14.7	−0.1	−2.3	737.9
WR4	0.72	0.1	752.8	15.2	−0.07	−2.65	733.8
WR5	0.48	0.1	755.2	15.3	−0.05	−2.99	736.9
WR6	0.3	0.1	748.2	16.2	−0.03	−3.5	729.2
WR7	0.41	0.07	752.3	15.8	−0.03	−3.5	723.9
WR8	0.61	0.22	764.7	15.2	−0.14	−1.96	756.4
WR9	0.49	0.06	742.9	16	−0.03	−3.5	713.4
WR10	0.33	0.14	746.9	16	−0.05	−2.99	734.0
WR11	0.51	0.06	765.5	15.8	−0.03	−3.5	735.6
MB0	0.76	0.07	753.6	13.8	−0.05	−2.99	727.4
MB1	0.35	0.09	756.5	14.3	−0.03	−3.5	736.9
MB2	0.68	0.08	745.5	15	−0.05	−2.99	722.6
CW0	1.44	0.01	713.7	14.6	−0.01	−4.6	502.9
CW1	0.57	0.07	757.7	14.1	−0.04	−3.21	730.4
CW2	0.26	0.08	758.2	14.6	−0.02	−3.91	736.2
CW3	0.3	0.13	752.5	14.6	−0.04	−3.21	738.2
CW4	0.29	0.05	760.7	14.6	−0.02	−3.91	726.9
CW5	0.28	0.22	757.1	14.7	−0.06	−2.81	748.6
CW6	0.55	0.08	744.2	14.8	−0.05	−2.99	722.2
CL0	0.6	0.27	755	13.3	−0.16	−1.83	748.1
CL1	0.43	1.2	751.3	13.9	−0.52	−0.65	749.7
CL2	0.82	0.05	757.7	13.8	−0.04	−3.22	719.4
CL3	0.4	0.77	749	14	−0.3	−1.2	746.6
CL4	0.34	0.6	753.8	14.4	−0.2	−1.61	750.7
CL5	0.49	1.24	750.2	14.7	−0.6	−0.51	748.7
CL6	0.38	1.74	749.4	14.7	−0.66	−0.42	748.4
CL7	0.5	12.9	745.1	15.1	−6.47	1.86	745.0
CL8	0.56	0.11	752.2	15	−0.06	−2.81	735.6

Retrieved values to the fitted parameters as well as the upwelling temperature gradient and t_c are shown in Table 4. All data indicate a negative temperature gradient. Two examples of the sigmoid-like function fit to data (DT3 and WR2) are shown (Fig. 10), and provide some confidence to the choice of function and the relation to the retrieved parameters in Table 4. Also, the event appears to start at WR2 before DT3 with the calculated t_c being hr 740 and 747 for WR2 and DT3, respectively, consistent with inspected values. Inspection of all the fits (not shown) indicates that the sigmoid-like function fit the data from all sites well, with the exception of CW0. The CW0 data had the largest amplitude and smallest temporal gradient retrieved. Examination of the data (Fig. 2) indicates that CW0 data are not appropriately characterized with the function in Eqn. 1.

In Fig. 11 are plotted retrieved upwelling temperature gradient versus amplitude. The natural logarithm of the negative of the gradient is used to reduce dynamic range for plotting purposes. I can see that the leeward seabed sensors, including those from the DTCTA

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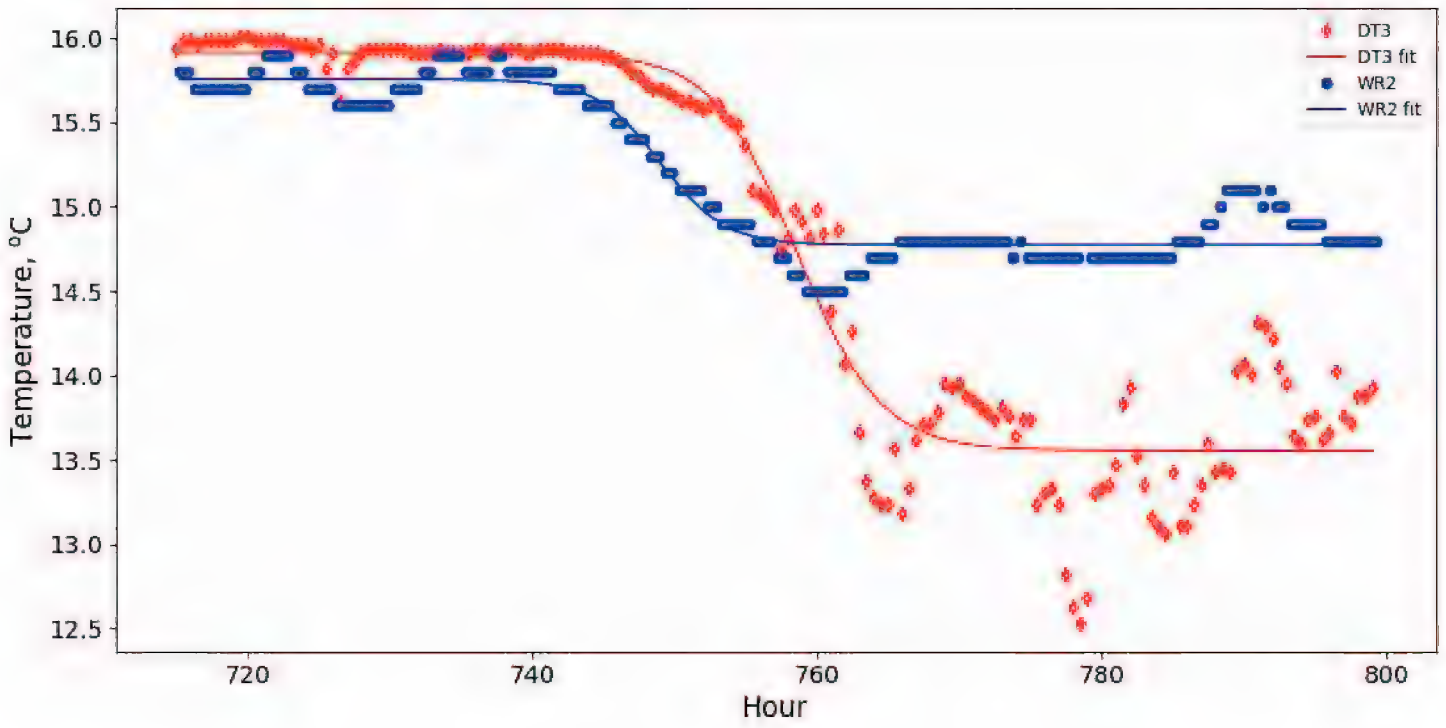

Fig. 10. Two examples of fits to temperature time series.

and CINP leeward sites exhibit characteristics that separate them from the buoy near-surface measurements and CINP windward sites. All but two leeward sites (12 out of 14) had a natural log value > -1.8, i.e., $\frac{\partial T}{\partial t} < -0.16$ °C hr^{-1} ($|\frac{\partial T}{\partial t}| > 0.16$ °C hr^{-1}) and all other sites had gradient magnitudes, $|\frac{\partial T}{\partial t}|$, <0.16 °C hr^{-1}. Of the four wave-rider sites with the largest gradients: WR0, WR3, WR4 and WR8, the latter three are in relatively shallow water (Table 3), being 23 m, 66 m and 20 m deep respectively. That is, the seabed depths are similar to the DTCTA site depths.

Computed commencement times, t_c, for DTCTA data appear to match well with those determined from data inspection (Fig. 3). Although the commencement time computation is expected to provide a noisy estimate, especially if the amplitude and temporal derivative are small, there are illustrative trends seen in Table 4. The open-ocean and windward sites'

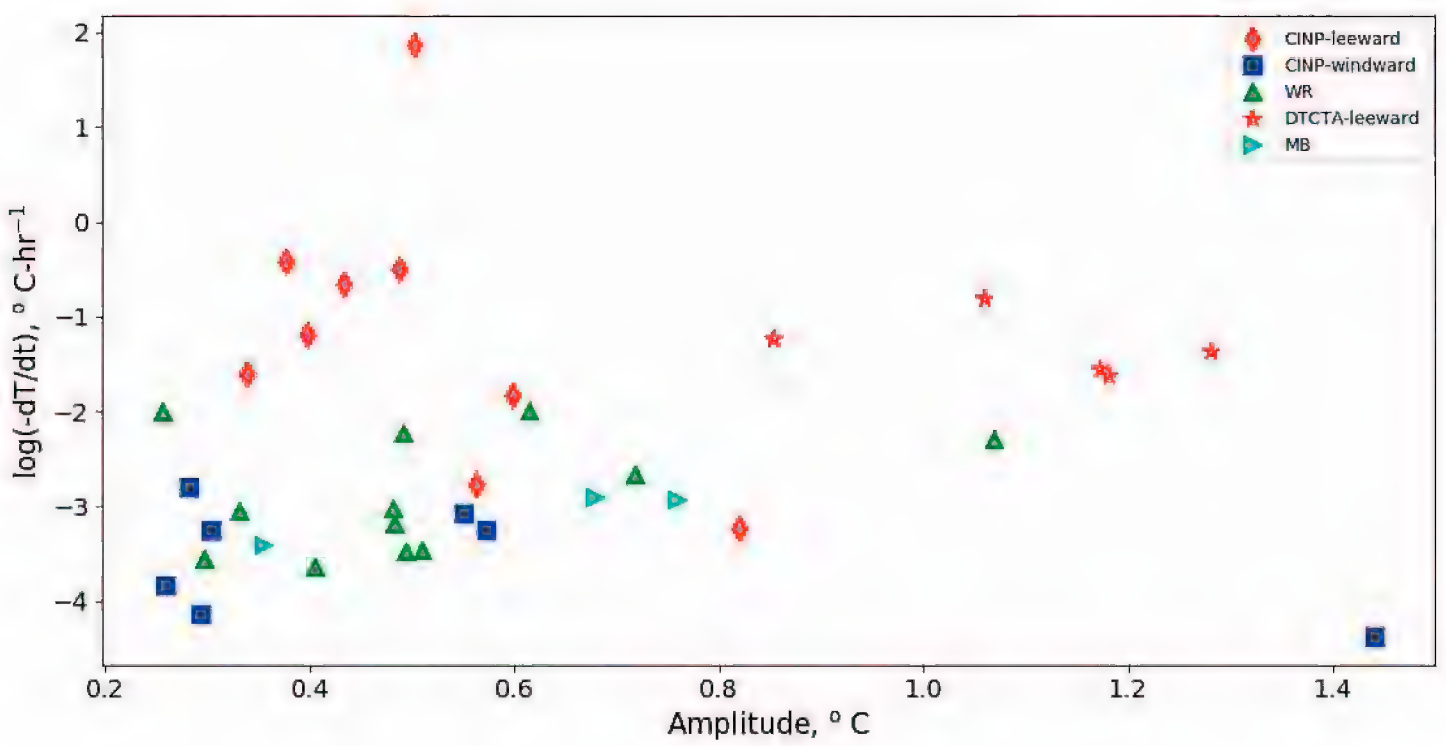

Fig. 11. Retrieved values of upwelling temporal gradient versus retrieved amplitude.

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commencement times precede those of the leeward sites. For example, the average t_c for the CINP leeward sites is hr 743, while for CINP windward sites (excluding CW0) is hr 733. Similarly, average t_c for the DTCTA is 748, while for the meteorological buoys is 729 and wave-rider buoys is 734. Hence, the upwelling expressions for the event occur later for the leeward sites, and the commencement times for the open-ocean and windward sites coincide roughly with the start of the wind event.

Discussion

Using the measurements described above, I address the issues stated in the introduction and place them in context with previous studies. First, I estimate the amount of upwelling and nutrient change, restricting my attention to the mainland coast where the Chl a response was prominent. The DTCTA-measured change in water temperature from 15.5 °C to 12.5 °C (Fig. 2) can be used in conjunction with the CalCOFI temperature/depth profiles to estimate the amount of upwelling. I assume that the CalCOFI profiles, measured nearly three weeks before the event, are representative of those at the beginning of the event. They were measured well before both the spring transition (Strub et al. 1987; Lynn et al. 2003) and the time when surface warming becomes significant (Gelpi and Norris 2008). The profiles (Fig. 7) indicate that 12.5 °C water was located at 100 m depth. Therefore, the upwelling shoaled water from this depth to the 10 m depth of the shallower thermographs, or a vertical distance of 90 m.

If upwelling commenced with the wind, hr 735, then in 9 hr, the entire mixed-layer depth (50 m below the 9.3 m DTCTA sensors) was upwelled to 10 m depth, at which time the temperature at the thermograph began to drop. The temperature decrease ended at hr 767, with nominal 100 m water reaching 10 m depth. This is an average vertical advection speed of 0.0008 m/s. For comparison, off the central coast, Jacox et al. (2014) give the mean upwelling velocity as on the order of 1 m/d, i.e., 1.2×10^{-5} m/s, or nearly two orders of magnitude lower, and Largier et al. (2003) infer a velocity of 1.2×10^{-4} m/s during a specific upwelling event. Hence, the 31 January event was large in comparison. The 58 m depth of the thermocline corresponded to the nutricline. Therefore, the upwelling brought significant nutrients to the upper water column. For example, the nitrate concentration increased by 1 to 2 orders of magnitude, from ~0.5 μM/l to 15 μM/l (Fig. 7).

Second, I want to develop insight into the upwelling mechanism. However, the upwelling characteristics clusters (Fig. 11) indicate that there could be several upwelling mechanisms. Among the leeward sites, I note that the DTCTA sites experienced larger amplitudes than the leeward CINP sites. CINP sites were colder than DTCTA sites before the upwelling (Fig. 3). Nearby CalCOFI profiles (not shown) indicated similar water temperatures at depth. If other factors are similar, such as wind forcing, then I expect DTCTA sites to have larger amplitudes simply because the temperature gradient with depth is larger, and therefore, both amplitude regimes could be accommodated with the same upwelling mechanism. There is also a disparity between temperature characteristics of leeward and windward/open-ocean sites. The windward/open-ocean sites reacted quicker to the wind than did the leeward sites and also their change in water temperature was less. Although the open-ocean locations measure the temperature near the surface and the CINP windward stations measure at depth, qualitatively similar results are obtained from both, suggesting the same upwelling mechanism for both open-ocean and windward locations. Hence, I just consider two upwelling mechanisms applicable to either leeward and windward/open-ocean sites.

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There are many physical mechanisms that can produce wind-induced upwelling in the SCB. These include propagation of coastally trapped waves, divergence due to flow past topography (Roughan et al. 2005), enhanced vertical mixing due to wind-generated turbulence, deep-water replacement of Ekman-transported water away from the coast, and shoaling of deep water to replace surface waters that are directly wind-advected from the coast. Coastally trapped waves are typically generated to the south of the SCB (Pringle and Riser 2003) and would not be coincident with the wind event nor would their effects be found simultaneously at diverse stations due to finite propagation speeds. Divergent flow past topographic features, e.g., the Palos Verdes Peninsula, may contribute to upwelling. But neither the temperature nor biological response (Fig. 8) appear to be localized to such topographic features, so these mechanisms are not considered further. Liang et al. (2009) have attributed vertical mixing to lower SST in their analysis of ocean response to high-frequency wind events in mountains gaps in Central America. This effect may be the mechanism for lowering the temperature at stations with large wind fetch (the windward and open water stations) in our event as the significant wave heights (not shown) generated by the wind reached 6 m, with enhanced vertical mixing expected. However, leeward sensors are within the wind shadow of the coastal and island mountains, providing little fetch for wave generation and direct turbulent mixing.

Ekman transport has been attributed by Dong et al. (2011) as the mechanism of upwelling for a somewhat similar SCB event occurring in mid-March 2002. They numerically analyzed the ocean geophysical response to modeled alongshore wind conditions through integrating the primitive equations. They were primarily interested in SST measurements which indicated a coastal temperature decrease of similar magnitude as found in the 2016 event described here. Their event occurred in a stratified ocean over a much longer timespan, $\sim$ 6 d, and inspection of their buoy data (corresponding to MB2 in this paper) indicates an upwelling temporal gradient of -0.02° hr^{-1}. This value is similar to the -0.05° hr^{-1} listing in Table 4 for this location in the event studied here. However, as described below, there are significant differences between the 2002 event and the one described here, suggesting different upwelling mechanisms may be appropriate.

The final proposed mechanism may be important along the leeward coasts where the seabed depth is less than the depth of the Ekman layer (that depth where the wind-induced current is orthogonal to the wind) and for short time scales that preclude achieving geostrophic balance, thereby producing relatively large shoaling directly off the coast. The offshore component of wind drags the surface waters away from shore, being replaced with deeper, colder water. This is the phenomenon observed by beach divers during Santa Ana winds mentioned in the introduction.

As mentioned, upwelling for open-ocean and windward coasts differed from that of the leeward coasts. The storm brought cooler air ($\sim$10 °C, Fig. 4) and larger waves, so near-surface cooling may represent the chilling of the surface and subsequent mixing of the colder water to sensor depth (which is nominally within the mixed layer). This would be expected to happen on a shorter time scale than the upwelling described above for the leeward coastal sensors. The commencement times being near the start of the wind event supports this argument. On the other hand, expectations are that the at-depth CINP-windward sites would experience delayed commencement times relative to the near-surface buoy measurements because of the time for mixing to achieve depth. But this delay is not found in the data. Mixing could be rapid at windward seabed sensors located near the surf zone as the SWH was an appreciable percentage of the depth, but this determination is outside the scope of this work. Such wind-wave-induced mixing is not expected to significantly

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increase the nutrient supply within deep mixed layers and I would not expect to measure greatly increased Chl a in these locations. This is consistent with the observed result as that Chl a increased much less in the windward/open-ocean locations as compared to the mainland leeward locations.

Third, I want insight into the upwelling relaxation mechanism which impacts nutrient availability. DTCTA measurements indicate relaxation back to pre-impulse temperatures after 11 d. The specific relaxation mechanism determines the availability of nutrients after the impulse. At least three mechanisms are contemplated: water warming via insolation or atmospheric heat flux; lateral advection of displaced warm water back to the coast; and, mixing of offshore warm water with nearshore cold upwelled water. The first mechanism does not directly change the nutrient concentration. The second mechanism replaces nutrient rich water with the original less nutritious water, while the third mechanism dilutes the near-coast nutrients.

The relaxation mechanisms can be discussed via the one-spatial-dimension diffusion-advection equation

$$\frac{\partial T}{\partial t} = S + v\frac{\partial T}{\partial x} + \mu\frac{\partial^2 T}{\partial x^2} \qquad \text{Eq. 2}$$

where S is a source, such as insolation, etc, x is the offshore distance coordinate, v is the advection velocity and μ is the horizontal eddy diffusion coefficient. A one-dimensional cross-shore model is considered as the temperature gradient seems to be independent of the along-shore distance as all the station measurements in DTCTA behaved similarly. I estimate the left-hand-side single term in Eqn. 2, i.e., the relaxation temporal derivative, for DT0 was $2.315\text{x}10^{-6}$ °C-s^{-1} ($8.33\text{x}10^{-3}$ °C-hr^{-1}).

Focusing on the source term in Eqn. 2, I note DTCTA measurements indicate relaxation back to pre-impulse temperatures after 11 d. The relaxation mechanism suggested by Dong et al. (2011) is warming produced by insolation. As they were examining SST rather than at-depth temperature and their analyzed event was in March when insolation is greater than in the February event, their mechanism suggested for relaxation may differ from the one applicable here. Liang et al. (2009) attribute the rapid relaxations (on the order of a few days) in their statistical study to a positive (into the ocean) heat flux limited to the upper-water column. A positive heat flux from either insolation or atmosphere-ocean energy transfer would develop a stratified ocean that I do not see in the Laguna (DT3 and DT4) data. Indeed, net heat flux into the water column is unlikely to produce the observed temperature increase (>2 °C) throughout the water column to 18 m depth. Using long-wave radiation, short-wave radiation, sensible and latent heat fluxes for this area as summarized in Gelpi and Norris (2008) (net flux <10 W m^{-2} during this time of year), hundreds of days are required to heat the water column by 2 °C, much longer than the measured 11 d. Hence, neither insolation nor atmospheric-oceanic heat exchange can quantitatively produce observed relaxation, so I regard S in Eqn. 2 as insignificant in the relaxation process.

To evaluate the other 2 terms on the right-hand-side of Eqn. 2, I need the offshore temperature gradient. I estimate the gradient using the 3 stations DT0, MB2 and CL7 which lie on a longitudinal line nearly perpendicular to the coast (Fig. 1) with distances to shore being 0.1 km, 33.6 km and 66.7 km, respectively. Although the station sensors are at different depths, the DTCTA Deadman data (DT3 and DT4) indicate the water column is well mixed so the temperature is independent of depth at this time, and the CalCOFI data indicate it was well mixed everywhere at the time of its measurements. From slightly smoothed

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times series, I estimate the temperature at hr 768, the start of relaxation, for these stations to be 12.5 °C, 14.3 °C and 15.6 °C, respectively. Using a quadratic fit to the 3 temperature values as a function of cross-shore distance, I find the quadratic, linear and offset coefficients are -2.1×10^{-10} °C m^{-2}, 6.0×10^{-5} °C m^{-1} and, of course, 12.5 °C, respectively. Using the relaxation temporal derivative, I can evaluate the eddy diffusion coefficient in Eqn. 2, assuming $v = 0$, to get $\mu \sim 5500$ m^{2}s^{-1}, or conversely, assuming $\mu = 0$, evaluate the advection velocity to be ~ 0.04 ms^{-1}. Of course, there would be a combination of advection and diffusion that produces the relaxation, but the derived extreme values are used for further discussions below.

The eddy diffusion coefficient, μ, value calculated above is consistent with values obtained from a variety of techniques, for example, tracking drifting buoys (Bauer et al. 2003), open-ocean tracer experiments (Banyte et al. 2013) and SST studies (Ostrovskii and Piterbarg 1995). Although a combination of advection and diffusion may be occurring, the low advection speed, when compared to typical California Current speeds of 0.25 ms^{-1}, does not appear to be a significant driver of the relaxation. Hence, I suggest that lateral mixing is the relaxation mechanism.

Fourth, I want to quantify and understand the biological response to the upwelling. There was a biological response as measured in Chl a, associated with the upwelling throughout the bight that also was stronger along the immediate coast and quantified in the Results section. Changes in the surface chlorophyll are not attributed to vertical advection of a chlorophyll gradient as the CalCOFI data did not indicate a gradient, i.e., there was no Deep Chlorophyll Maximum in the depth profile. The relative differences in Chl a in the middle of the bight and along the Los Angeles border mirror the changes in temperature at the two locations, and suggests that the two proposed upwelling mechanisms for respective leeward and windward sites profoundly affect the amount of Chl a produced.

The response lasted only about one week or less. As the Chl a measurement resolution was 8 d, shorter response times could not be measured. This time scale is consistent with results from Nezlin et al. (2012), who report increased Chl a values lasting 5-8 d after upwelling events. The short-temporal biological response contrasts to the spring transition, which at Santa Catalina Island was statistically determined to be 60 d using Aqua/MODIS Chl a product (Gelpi 2018), and occurs later in the year, starting about March 1. During the transition, equatorward flow is noted in the SCB (Bray et al. 1999), similar to flow computed by Dong et al. (2011) and perhaps indicative of more continuous upwelling. Relaxation during the spring transition may appear to be slower as upwelling events may be more continuous and long lasting, as in the case study of Dong et al. (2011). The swift relaxation in our event that replaces the nutrient-rich water with less nutrient-rich water may be the cause of the rapid Chl a decrease as phytoplankton would have less nutrients to enable growth. However, this interpretation differs from Wilkerson et al. (2006), who, in an analysis of upwelling off the central coast, indicated phytoplankton consumption depleted nitrate supplies sufficiently to reduce the Chl a signal on the measured time scale. This biological relaxation mechanism, however, would not increase the water temperature at depth as I found for this event.

Conclusions

High offshore winds associated with a winter storm resulted in significant upwelling along the coast and colder water throughout the bight as measured by *in situ* sensors. On the leeward side of the coasts, both mainland and island, the upwelling temperature signal

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appeared impulse-like with large temperature temporal gradients and large amplitudes, especially off the mainland. Temperature measurements made at open-water and windward locations exhibited much smaller amplitudes and temporal gradients. Changes in temperature at leeward sites was also delayed by ~10 hr relative to the other sites. Differing amplitudes, time scales and commencement times suggest different upwelling mechanisms between the leeward and other sites. I speculate that the leeward sites experienced shoaling deep water that replaced the wind-advected surface water after the mixed layer was removed, while the other sites may have experienced a more immediate cooling due to cooler air temperatures chilling the surface which is then mixed to depth via wind turbulence. Based on CalCOFI results, the mainland leeward nearshore water shoaled approximately 90 m, bringing the thermocline and coincident nutricline to the surface. Increases in Chl a values from remotely-sensed satellite data indicated a biological response was largest next to the mainland coast. Both the Chl a and temperature relaxed to pre-storm values within 11 d. The relaxation time scale is consistent with horizonal eddy diffusion rates, mixing offshore warmer water with the near-shore upwelled water, reducing nutrients and inhibiting phytoplankton growth to limit the biological response.

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Prioritizing the Risk and Management of Introduced Species in a Landscape with High Indigenous Biodiversity

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Abstract.—Risk analysis protocols for prioritizing the management of non-native species are numerous, yet few incorporate risk and management in the same analysis or accommodate a broad diversity of taxa outside of a specific geographic area. We adapted a protocol that accounts for these factors to address non-native animal species in the Southern California/Northern Baja California Coast Ecoregion near the international border in San Diego County, an area with high indigenous biodiversity and high numbers of species of conservation concern. This stepwise, semi-quantitative protocol is applicable to any animal group in any predefined geographic area, relies on consensus-building among taxonomic experts, and has been vetted through previous use and in peer-reviewed literature. Our results show that the final prioritization was driven mainly by management feasibility, with top-ranked species having multitrophic effects that favor other non-native invaders over native residents. Conditions within the assessment area required some modification to the protocol as it was originally designed, namely a shift in emphasis from eradication to control, given that eradication is implausible for most non-native species in the assessment area. We call attention to taxon-specific issues that surfaced during the analysis, identify areas for improvement in this first-ever risk assessment for invasive animal species in the Natural Communities Conservation Plan/Habitat Conservation Plan (NCCP/HCP) reserve system of San Diego County, and provide suggestions for further refinement of the protocol. This study builds on the effort to standardize risk analysis for invasive species globally, given that many of the same invaders present threats to indigenous biodiversity worldwide.

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Managing non-native species in their introduced environment requires careful prioritization given the large number of species that present threats, the high costs associated with management, and the limited resources for enacting control measures (Hulme 2009; Roy et al. 2014; Early et al. 2016; McGeoch et al. 2016). Protocols have typically involved one of two approaches; risk assessment, which evaluates the threats posed by different species, or risk management, which evaluates the effectiveness of different management options (see reviews in Verbrugge et al. 2010; Leung et al. 2012; Roy et al. 2014). Numerous risk assessment protocols have been developed, but most are focused on specific taxonomic groups in a predefined geographic area, and many do not incorporate management potential in the overall assessment (Vanderhoeven et al. 2015). Of those that incorporate risk assessment and management in the same protocol (e.g., in countries like Australia and New Zealand [Virtue et al 2006; COAG 2012] and the European Union [Booy et al. 2020]), more effort is needed to ensure that consistent criteria are implemented among researchers globally (Brunel et al. 2010; Booy et al. 2017) given that many of the same invaders are negatively impacting ecosystems worldwide (Lowe et al. 2004).

Prioritizing efforts to combat non-native species is critical for areas with high indigenous biodiversity and-or a high proportion of rare and declining species (Myers et al. 2000; Li et al. 2016). For these reasons, biological invasions have been problematic in the Southern California/Northern Baja California Coastal Ecoregion near the US/México border in San Diego County. Vulnerability of the native fauna and flora is exacerbated by urban sprawl and commerce around the cities of San Diego and Tijuana (Cadotte et al. 2017), which facilitates new invasions and intensifies the effects of invaders that are already established (Suarez et al. 1998; Bolger et al. 2000; Riley et al. 2005). Routes of entry include: (1) unaided dispersal from a nearby area or as part of an expanding front, or (2) human assistance that was either accidental (e.g., hitchhiking in shipments of nursery stock, sod, agriculture, or infected firewood, escaped livestock, and bait spillover from sportfishing) or deliberate (e.g., for hunting/fishing, biological control, or release of unwanted pets). Fortunately, a considerable portion of coastal San Diego County falls within the Natural Communities Conservation Plan/Habitat Conservation Plan (NCCP/HCP) reserve system, a set of protected lands developed in coordination between state and federal wildlife agencies that borders, and in some cases interdigitates, with the urban matrix (Fig. 1). Due to its high connectivity and extensive urban edges, the reserve system benefits from maintenance and concerted efforts among partners to curb further spread and damage caused by non-native species.

To consolidate efforts across the NCCP/HCP and San Diego County more broadly, the San Diego Management and Monitoring Program (SDMMP: https://sdmmp.com/index.php) was tasked with creating a strategic habitat plan to define conservation objectives and generate benchmarks for success (the Management Strategic Plan [MSP] roadmap, available at https://sdmmp.com/msp_doc.php). One of these objectives was to identify and prioritize the management of non-native terrestrial and freshwater animal species. To fulfill this goal, a practical approach was needed to address the diversity of animals that either threaten or have high potential to threaten local biodiversity (Simpson and Eyler 2018). The sheer number and diversity of taxa led to the realization that progress could only be achieved through a standardized methodology that was applicable across taxa.

To this end, we employed an adaptive protocol that incorporates both risk assessment and management potential and is theoretically applicable to any animal group in any predefined geographic area (developed in Baker et al. 2005, 2008; Roy et al. 2014; Booy et al.

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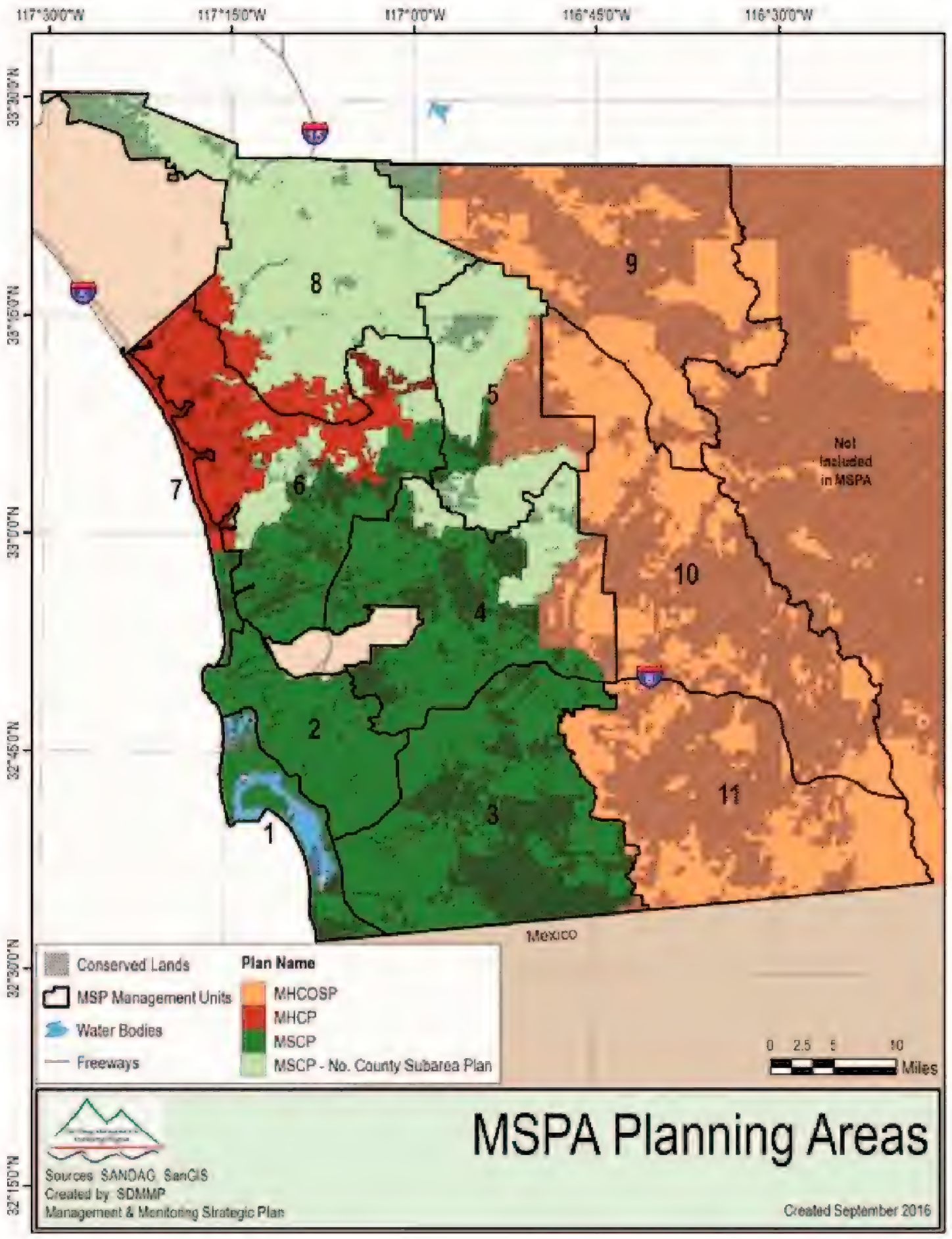

Fig. 1. Geographic area covered by the MSP Roadmap ('MSP Area' or 'MSPA'). The roadmap area is divided into 11 management units comprising 250,905+ ha of preserve lands, all of which fall within an approved or proposed large-scale Natural Communities Conservation Plan/Habitat Conservation Plan (NCCP/HCP) reserve system. Plans depicted are the San Diego Multiple Species Conservation Program (MSCP), San Diego Multiple Habitats Conservation Program (MHCP), the Multiple Habitat Conservation and Open Space Program (MHCOSP), and the proposed San Diego North County Plan (MSCP – North County subarea plan).

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2017). This non-native risk management protocol (hereafter NNRM following Booy et al. 2017, 2020) follows a stepwise, semi-quantitative procedure that relies on consensus building among experts to reduce subjectivity and bias. It also avoids arbitrary scoring and weighting schemes that would otherwise be needed to address disparate taxonomic groups (Bolger and Rowe 2015). At its core, high-risk species that can be contained at lower cost and effort take precedence over other high-risk species where management is predicted to be costly and/or ineffective. This protocol has been vetted in the peer-review scientific literature and modified and refined through use since 2005 (http://www.nonnativespecies.org; Booy et al. 2017, 2020).

Two of the most appealing aspects of the NNRM protocol are that (1) it can be tailored to any predefined geographic area, and (2) the assessments it generates can be modified as new knowledge or opinions surface, threat levels change, or if new introductions occur. This was key given that this risk assessment represents a first attempt at strategic management planning for non-native species on preserve lands within San Diego County, California. Our goals were twofold: (1) to use the NNRM in building toward a consensus for how researchers assess the risk of non-native species in different parts of the world; and (2) to develop a prioritization for mitigating the establishment or further spread of non-native species on protected lands within a global biodiversity hotspot (Myers et al. 2000).

Materials and Methods

We considered 'non-native species' to be any species that has been introduced outside of its natural range into San Diego County. In general, we did not evaluate species that were introduced elsewhere then subsequently dispersed into the study area without human agency, unless they were considered to be a serious threat to native species/habitat or were not already being actively managed (see below for further discussion). The scope of work included the following animal groups: fishes, amphibians, non-avian reptiles, birds, mammals, mollusks (gastropods [Gastropoda] and bivalves [Bivalvia]), annelids (Clitellata), flatworms (Rhabditophora), and arthropods (spiders [Arachnida], insects [Insecta], and crustaceans [Malacostraca]). Although amphibians and non-avian reptiles do not form a natural evolutionary group, we evaluated them collectively (hereafter herps) because they fall within a common field of study (i.e., herpetology) and all herpetologists recruited for this project had considerable expertise with both groups.

The SDMMP requested that the U.S. Geological Survey (San Diego Field Station, hereafter USGS) manage the following four stages of the analysis (Fig. 2): (1) generating a list of non-native taxa and reference material relevant to assessing risk and management actions; (2) identifying and communicating with potential assessors/taxonomic experts about participation in the project; (3) completing the risk assessment and management questionnaires for as many species as possible on the target list, focusing first on those that present the greatest threats to biodiversity on conserved lands; and (4) conducting a consensus building workshop to arrive at a final prioritization across taxa. We briefly describe each of these stages below.

Stage 1, Non-native species inventory list.—A description of the Southern California/Northern Baja California coastal ecoregion is presented in Griffith et al. (2016), and the study area within this region is depicted in an ArcGIS map viewer of San Diego County supported by the SDMMP (https://sdmmp.com/gis_viewer.php). From within this area (Fig. 1), we first assembled an inventory of non-native species by taxonomic group

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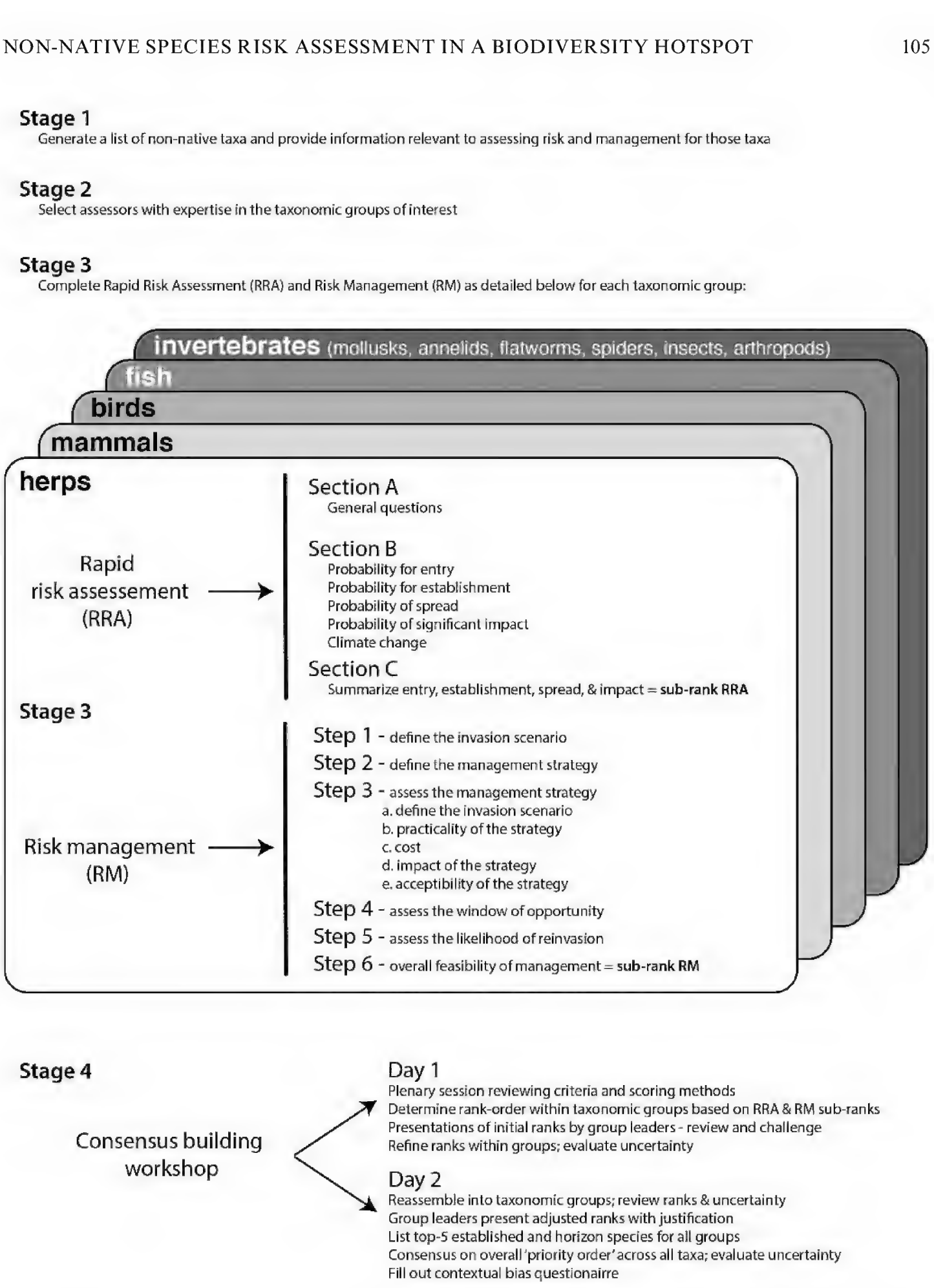
Stage 1
Generate a list of non-native taxa and provide information relevant to assessing risk and management for those taxa
Stage 2
Select assessors with expertise in the taxonomic groups of interest
Stage 3
Complete Rapid Risk Assessment (RRA) and Risk Management (RM) as detailed below for each taxonomic group:
invertebrates (mollusks, annelids, flatworms, spiders, insects, arthropods)
fish
birds
mammals
herps
Rapid risk assessement (RRA)
Section A
General questions
Section B
Probability for entry
Probability for establishment
Probability of spread
Probability of significant impact
Climate change
Section C
Summarize entry, establishment, spread, & impact = sub-rank RRA
Stage 3
Risk management (RM)
Step 1 - define the invasion scenario
Step 2 - define the management strategy
Step 3 - assess the management strategy
a. define the invasion scenario
b. practicality of the strategy
c. cost
d. impact of the strategy
e. acceptibility of the strategy
Step 4 - assess the window of opportunity
Step 5 - assess the likelihood of reinvasion
Step 6 - overall feasibility of management = sub-rank RM
Stage 4
Consensus building workshop
Day 1
Plenary session reviewing criteria and scoring methods
Determine rank-order within taxonomic groups based on RRA & RM sub-ranks
Presentations of initial ranks by group leaders - review and challenge
Refine ranks within groups; evaluate uncertainty
Day 2
Reassemble into taxonomic groups; review ranks & uncertainty
Group leaders present adjusted ranks with justification
List top-5 established and horizon species for all groups
Consensus on overall 'priority order' across all taxa; evaluate uncertainty
Fill out contextual bias questionairre

Fig. 2. Steps for implementing the risk analysis. RRA and RM templates should be completed for both established and horizon species in each taxonomic group.

(Supplemental Data—'Invasive species list') and then assigned each species to one of two categories, either 'established' or 'horizon'. We recognized the following distinctions for established species: (1) *Established and widespread*—species with reproducing populations in more than one watershed and recorded frequently; (2) *Established but limited*—species that have been documented repeatedly for ~10 or more years (indicating establishment), but records are predominantly from dispersed localities within a single watershed;

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(3) *Reported but undetermined*—species reported in one to several localities over time but essentially nothing is known about their status (e.g., a few records at www.inaturalist.org, a website recording crowdsourced species identifications and occurrences); (4) *Extirpated*—species that were once present but are no longer in San Diego County, either because of purposeful eradication or they have not been detected following 5+ years of surveys.

We defined horizon species as those that are (1) undocumented in the study area but have been recorded in adjacent counties in California or northern Baja California and are causing ecological damage; and/or (2) have a reasonable chance of being introduced through a frequent vector (e.g., aircraft, shipping cargo, etc.), are causing ecological damage in its introduced range, and could become established in the study area due to favorable environments (see Kahl et al. 2012 for a case involving an invasive snake). An example of #2 in this study was the Small Indian Mongoose *Urva auropunctata*, which runs the risk of being transported to San Diego through frequent commercial/military aircraft and shipping cargo from Hawai'i. In Hawai'i and elsewhere in its introduced range, *U. auropunctata* is an invasive predator on a wide variety of taxa – should it reach San Diego, the species could potentially have devastating effects on the region's native birds, amphibians, reptiles, and small mammals (Berentsen et al. 2017; Louppe et al. 2020).

We evaluated established (widespread, limited, reported but undetermined) and horizon species separately but used the same assessment templates to perform the analysis for each group. Species that are extirpated did not receive formal treatment beyond inclusion on the species list, unless the assessors agreed that there was strong chance of reintroduction. We did not address agricultural pests because the MSP Roadmap applies to conserved lands, unless the species had spillover effects. We also did not consider the non-native earthworms (Annelida: Oligochaeta) from Europe, Asia, and South America due to the large number of species that have been reported in California ($n = 35$) and because little is known about their statuses and effects on native flora and fauna (Wood et al. 1993; Reynolds 2019). Last, certain species that are already being actively managed at the county-wide or larger geographic scale did not receive formal treatment in this analysis (e.g., *Aedes* mosquitoes; Metzger et al. 2017).

The categories for 'established' were not part of the original NNRM protocol, but we considered them necessary given the broad taxonomic scope of our assignment (i.e., animal species), the large number of non-native species in San Diego County, and the fact that this was a first attempt at performing a risk assessment for NCCP/HCP lands. We view this assessment as a starting point, with further refinements anticipated as more knowledge is acquired over time.

Stage 2, Selecting assessors.—We selected assessors based on taxonomic expertise using literature searches, personal knowledge by one or more of the USGS participants, and/or by reputation from trusted sources. We prioritized those having familiarity with the fauna of southern California, and those who were within a reasonable travel distance to the USGS San Diego Field Station to reduce cost. Assessors were organized into taxon-specific groups comprised of a leader and variable numbers of participants. We attempted to adjust the number of assessors such that groups with higher numbers of species had proportionately more assessors. The final working group included museum curators and associates, university professors, graduate students, biological consultants, and employees of various state and federal government agencies.

Stage 3, Templates for risk assessment and risk management.—We summarized the risk-assessment and risk-management templates below, which were adapted from Booy et al. (2017). Slight modification to the original verbiage was aimed at capturing local

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conditions within San Diego County. Blank templates for ranking species (see below for details: (RM_template_v1.2; RRA_template_v1.2), guidance for answering the questionnaires, and descriptions of some additional modifications to the original protocol are provided as electronic supplemental files (Supplemental File protocol_mods).

Prior to the workshop, we requested that each assessor complete templates for one to three species after reading a tutorial of the protocol (Fig. 2). We provided examples of completed templates to help standardize the level of detail for each species. Templates could be filled out using web- and literature-based searches or expert judgment, with reference material documented in the templates. In certain cases, we improved efficiency by summarizing multiple species under a single template, such as those with similar demography, ecology, behavioral tendencies, close evolutionary relatedness, or that could be managed in similar ways. Experts then verified whether these groupings were appropriate, and if not, the group was dissolved. Examples of groupings included the three closely related species of water snake (genus *Nerodia*), two species of shot hole borer (genus *Euwallacea*), and two species of anole (genus *Anolis*).

The risk-assessment scheme of Booy et al. (2017) is comprised two fundamentally similar versions: a short form '*rapid risk assessment*' (RRA; Supplemental File – RRA_template_v1.2) designed for a high volume of species and a rapid turnaround time, and the larger, more detailed '*risk assessment*' (RA). We used only the short form RRA for this analysis and suggest that the long-form RA be reserved for cases where explicit management or contentious policy decisions are imminent (Supplemental File RA_template_v1.2). The RRA is divided into three sections (Fig. 2). In Section A, assessors answered seven general questions ranging from where the species has been observed to the type of harm it inflicts (or could inflict) in the assessment area. Section B consists of summary statements about entry, establishment, spread, impacts, and the influence of climate change. Response categories range from 'very unlikely' or 'very slow' to 'very likely' and 'very rapid'. Section C contains a summary of the risk assessment.

Assessors then filled out the '*risk management*' template (RM; Supplemental File – RM_template_v1.2) for the same species (Fig. 2). Step 1 entailed a coarse description of how widespread the species currently is or will be at the point of detection. Step 2 defined the management strategy, which could include multiple control techniques (trapping, shooting, pesticides, etc.). Feasibility of control was then evaluated based on five questions related to effectiveness, practicality, cost, impact, and acceptability (steps 3a-e), followed by an assessment of the window of opportunity for interdiction and likelihood of reinvasion (steps 4 and 5). The last step (step 6) summarized the management potential and reflected expert judgment based on the previous five steps. For each question and the overall conclusion, a response ranging from 1 to 5 (least to most favorable) was supported by a written justification (see Table 1 for response criteria). Cost values are somewhat arbitrary and reflect previous field projects conducted on NCCP lands in San Diego County. The window of opportunity reflects time scales that are applicable to a wide range of taxa. Confidence in each response was based upon a three-point scale (low, medium, high).

The RRA and RM templates were used to generate sub-ranks for the risk and management feasibility of a given species; the two sub-ranks were then used to establish the rank of that species within its respective taxonomic group at the workshop. Those ranks were ultimately used to generate the overall prioritization across all taxa (Fig. 2). Both the rankings within a group and overall priority across groups were determined via deliberation and consensus among experts. To test whether risk factor was a predictor of management feasibility, we calculated the polychoric correlation ρ (and its standard error) between the

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Table 1. Assessment criteria for response scores associated with each of the six steps of the Risk Management (RM) template. Scores ranged from 1 to 5 (least to most favorable) for each criterion. Criteria relate to the effectiveness, practicality, cost, degree of negative impact, and acceptability (steps 3a-e) of a proposed management strategy for a given non-native species, the window of opportunity for successful interdiction, and the likelihood of reinvasion if control or eradication is achieved (steps 4 and 5). Step 6 summarizes the management potential and reflects expert judgment based on the previous five steps, supported by empirical data/references when available.

	Response				
Criteria	1	2	3	4	5
Effectiveness	Very ineffective	Ineffective	Moderate effectiveness	Effective	Very effective
Practicality	Very impractical	Impractical	Moderate practicality	Practical	Very practical
Cost	>$10M	$1.2–10M	$250K–1.2M	$65–250K	<$65K
Negative impact	Massive	Major	Moderate	Minor	Minimal
Acceptability	Very unacceptable	Unacceptable	Moderate acceptability	Acceptable	Very acceptable
Window of opportunity	<2 months	2 months–1 yr	1–3 yrs	4–10 yrs	>10 yrs
Likelihood of reinvasion	Very likely	Likely	Moderate likelihood	Unlikely	Very unlikely
Conclusion (feasibility of management)	Very low	Low	Medium	High	Very high

two ordinal scores for risk and feasibility of management using the maximum likelihood estimator in the Polychor package (Fox 2022: https://CRAN.R-project.org/package = polychor) in R (R Core Team 2017). This approach is similar to linear correlation, with the ML estimate of ρ ranging between 0 and 1 (where 0 = no relationship and 1 = perfect relationship: Olsson 1979). Significant correlation suggests that the two scores quantify similar information.

Stage 4, Consensus-building workshop.—This two-day exercise began with a plenary session in which all criteria and ranking methods were reviewed (see Supplemental File Workshop_Agenda_Instructions for a sample workshop agenda and instructions for participants). Experts then assembled into groups to develop the within-taxonomic-group rankings, and each group was assigned a scribe to record information. The scribes kept track of any controversies, problems in applying the protocol, and any changes in the rankings during deliberations. We asked that the following strategy be used as a starting point for rankings within a taxonomic group:

1. Of the taxa that are established (widespread, limited, and/or undetermined status), have each group member generate a risk ranking based on firsthand knowledge, then work toward a consensus through discussion and defense of the personal rankings (similar to jury deliberation in a court of law).
2. Take the top-5 species from the group's intuitive ranking from step 1 above and ensure that the RRA and RM templates are completed as thoroughly as possible for those species. We note that 'top-5' is an arbitrary cut-off for ranking species, but given the time, cost, and personnel limitations involved with this initial

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prioritization, participants agreed that this threshold was useful for focusing attention on species that pose the greatest risks (see also #5 below).
3. Modify the intuitive rankings if new information or opinions develop while considering the topics in both templates.
4. Repeat steps 1–3 for all horizon species in each assigned group.
5. If the top-5 established and horizon species are agreed upon by the group before the session is over, rank the next five established and horizon species, in that order, and proceed in the same manner until the session finishes.

The breakout sessions on Day 1 were followed by oral presentations from each group leader. These presentations were key to refocusing the directives of the protocol and helped to standardize how each group arrived at its decisions. Following these oral presentations, the groups then reassembled to discuss any adjustments to their initial rankings.

Day 2 began with the groups reassembling, followed by presentations of the adjusted within-group ranks to all participants. To facilitate presentations, we used the wall of a conference room partitioned into a matrix consisting of three rows and five columns, where rows represented the RRA sub-ranks and column headers represented the RM sub-ranks. Each group leader was given a colored set of notecards and wrote the names of the top-5 priority species for the group on a single notecard and place them within the matrix. We completed one round for established species and one for horizon species, and in each round, there was deliberation and rearrangement of species within the matrix. At the end of this process, response and confidence scores were agreed upon by all participants.

We recognize that consensus-based methods are susceptible to contextual biases, including dominance, overconfidence, anchoring and groupthink (see the discussion in Hanea et al. [2017] and Hemming et al. [2018]). These issues were discussed at the outset of the workshop; however, we ultimately relied on the participants to maintain an awareness of these potential biases throughout the consensus building process rather than attempting to build in avoidance measures to the protocol itself. At the end of the workshop, we provided an anonymous questionnaire that allowed participants to reveal any perceived biases that may have influenced decisions within and across working groups.

Results

We identified 51 priority species by the completion of the workshop. Of these, 29 are established on conserved lands in San Diego County and 22 are horizon species. Of the 51 priority- 'species', 11 were groups of taxa representing more than one species (see Methods section for rationale). Of these grouped entries, four were combined by the USGS prior to the workshop and seven were combined during the breakout sessions. We provide a brief description of the main threats identified for each taxonomic group in the Supplemental File. Table 2 summarizes the overall result of the prioritization across all species and represents the "to-do" list in terms of which species represent the highest potential priorities for control or eradication. The anonymous questionnaire at the end of the study revealed no cases of undue influence by any participants during the prioritization.

Groups with the greatest number of established high-risk taxa based on the RAA sub-ranks were as follows (highest to lowest; Table 3): Arthropods and fish (tied – 5/5 species were ranked as high risk); mammals (4/5 were high risk); herps and mollusks (tied – 2/5 species); and birds (1/5 species). Established species with the highest potential for management based on the RM sub-ranks were as follows (by group, highest to lowest): (1) herps (4/5 species were identified as having high potential for some level of control),

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Table 2. Overall prioritization across all established (A) and horizon (B) animal species based on risk and management feasibility. The first column represents the numeric equivalent of the overall priority (e.g., American Beaver *Castor canadensis* scored as '8 - Highest' given a risk assessment score (RA) = 3 ('high') + a risk management score (RM) = 5 ('very high').

A.

Priority	Species - established
8 - Highest	American Beaver (*Castor canadensis*)
8 - Highest	Redeye Bass (*Micropterus coosae*)
8 - Highest	Big-headed Ant/Red Imported Fire Ant (*Pheidole megacephala/Solenopsis invicta*)
7 - Very High	Fox Squirrel (*Sciurus niger*)
7 - Very High	Wild Boar (*Sus scrofa*)
7 - Very High	Prickly Sculpin (*Cottus asper*)
7 - Very High	Crayfish (*Procambarus sp.*)
7 - Very High	American Bullfrog (*Rana catesbeiana*)
6 - High	Domestic/feral cat (*Felis catus*)
6 - High	Largemouth Bass (*Micropterus salmoides*)
6 - High	Green Sunfish (*Lepomis cyanellus*)
6 - High	Goldspotted Oak Borer (*Agrilus auroguttatus*)
6 - High	African Clawed Frog (*Xenopus laevis*)
6 - High	Italian White Snail (*Theba pisana*)
6 - High	Black-throated Magpie-jay (*Calocitta colliei*)
6 - High	Wild Turkey (*Meleagris gallopavo*)
6 - High	Red-eared Slider/Painted Turtle (*Trachemys scripta elegans/Chrysemys picta*)
6 - High	Italian Wall Lizard/Green Anole, Brown Anole (*Podarcis sicula/Anolis carolinensis, A. sagrei*)
6 - High	Barred Tiger Salamander (*Ambystoma mavortium*)
5 - Moderate	European Starling (*Sturnus vulgaris*)
5 - Moderate	Shot Hole Borers (*Euwallacea kuroshio, E. witfordiodendrus*)
5 - Moderate	Argentine Ant (*Linepithema humile*)
5 - Moderate	Quagga Mussel (*Dreissena rostriformis bugensis*)
4 - Low	Black Bullhead (*Ameiurus melas*)
4 - Low	Channeled Apple Snail (*Pomacea canaliculata*)
3 - Very Low	House Mouse (*Mus musculus*)
3 - Very Low	Decollate Snail (*Rumina decollata*)
3 - Very Low	Greenhouse Slug (*Milax gagates*)
3 - Very Low	Scaly-breasted Munia (*Lonchura punctulata*)
3 - Very Low	Red-crowned Amazon, Lilac-crowned Parrot (*Amazona viridigenalis, A. finschi*)

B.

Priority	Species - horizon
8 - Very High	Red Fox (*Vulpes vulpes*)
8 - Very High	Mozambique Tilapia (*Oreochromis mossambicus*)
8 - Very High	Nanday Parakeet (*Aratinga nenday*)
8 - Very High	Yellow Crazy Ant (*Anoplolepis gracilipes*)
8 - Very High	Electric Blue Crayfish (*Procambarus alleni*)
7 - High	Nutria (*Myocastor coypus*)
7 - High	Pine Shoot Beetle/Ambrosia Beetles (*Tomicus piniperda/Xyleborinus andrewesi, Xyleborus glabratus*)
7 - High	Asian Long-horned Beetle (*Anoplophora glabripennis*)
7 - High	Grass Carp (*Ctenopharyngodon idella*)
6 - High	Pin-tailed Whydah (*Vidua macroura*)
6 - High	Mute Swan (*Cygnus olor*)
7 - High	Sonoran Spotted Whiptail (*Aspidoscelis sonorae*)
7 - High	Rio Grande Leopard Frog, Southern Leopard Frog (*Rana berlandieri, R. sphenocephala*)
6 - High	Egyptian Goose (*Alopochen aegyptiaca*)

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Table 2. Continued.

Priority	Species - horizon
6 - Moderate	Small Indian Mongoose (*Urva auropunctatus*)
6 - Moderate	Mississippi Silverside (*Menidia audens*)
6 - Moderate	New Zealand Mudsnail (*Potamopyrgus antipodarum*)
6 - Moderate	Zebra Mussel (*Dreissena polymorpha*)
6 - Moderate	Ferret (*Mustela putorius*)
5 - Low	Banded Water Snake, Northern Water Snake (*Nerodia fasciata*, *N. sipedon*)
5 - Low	Bluefin Killifish (*Lucania goodei*)
4 - Very Low	Red Shiner (*Cyprinella lutrensis*)
2 - Lowest	Japanese White-eye (*Zosterops sp.*)

(2) mammals (3/5 species had very high or high potential), 3) arthropods and fish (tied - 2/5 - one species had very high potential and one species had high potential), (4) birds (2/5 species had high potential) (5) and mollusks (0/5 had high potential).

Birds and fish were the only two groups with five horizon species total, arthropods and mammals had four, and herps and mollusks each had two. All horizon species of arthropods and mollusks were considered high risk, whereas bird and fish horizons spanned low to high, and herp horizons were all medium risk. Arguably the most concerning horizon species (i.e., in terms of worst-case scenarios if they were to invade) were those identified as high risk but with low potential for management. Four fell into this category – one mammal, the Small Indian Mongoose, one fish, the Mississippi Silverside *Menidia audens*, and two mollusks, the New Zealand Mudsnail *Potamopyrgus antipodarum*, and the Zebra Mussel *Dreissena polymorpha* – yet all were determined to be only 'moderate' priorities with regard to interdiction.

Visualizations of these rankings were displayed as heat matrices in Fig. 3. For established species, those posing the highest risk spanned the full range of categories for management feasibility, with most species having medium potential for some level of control (n = 6/19 high-risk species). Medium-risk taxa ranked either low or high on the management-feasibility scale, whereas low-risk species had either low or medium potential for management.

We found that the primary driver of the top-5 priority rankings within each taxonomic group was management feasibility. Table 4 provides the clearest representation of this finding by showing that the standard deviations of the RM sub-ranks were considerably more variable than the RRA sub-ranks, which tended to be more consistent within each taxonomic group. The polychoric correlation test also showed no significant relationship between risk and management feasibility scores ($\rho = 0.3985$, SE = 0.1662; test of bivariate normality $\chi^2 = 8.408$, df = 7, $p = 0.298$), indicating that the two metrics inform the analysis in different ways. We also found that the consensus-building approach had a strong influence on how species were ranked within groups between the time of the first oral presentation by group leaders (i.e., following only one within-group breakout session) to the end of the second oral presentations on Day 2 after multiple breakout sessions combined with deliberations among all assessors (Table 5).

Discussion

Given the wide range of approaches for analyzing the risk of non-native species, combined with the fact that many of the same species pose similar threats worldwide, we agree

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Table 3. Summary of the top-5 highest risk species for all taxonomic groups. Species are listed in descending rank order for each taxonomic group. RRA (risk) and RM (management) represent the template sub-ranks; RRA values range from 1-3 [low/medium/high]; RM values range from 1-5 [very low/low/intermediate/high/very high]). Grouped species that are of a different genus are separated by a slash, while grouped species of the same genus are separated by a comma.

Species	RRA	RM	Species	RRA	RM
Birds established			**horizon**		
Black-throated Magpie-jay	2 - Medium	4 - High	Nanday Parakeet	3 - High	4 - High
Wild Turkey	2 - Medium	4 - High	Pin-tailed Whydah	2 - Medium	4 - High
European Starling	3 - High	2 - Low	Egyptian Goose	1 - Low	5 - Very High
Scaly-breasted Munia	1 - Low	2 - Low	Mute Swan	2 - Medium	4 - High
Red-crowned Amazon, Lilac-crowned Parrot	1 - Low	2 - Low	Japanese White-eye	1 - Low	1 - Very Low
Fish established			**horizon**		
Redeye Bass	3 - High	5 - Very High	Mozambique Tilapia	3 - High	4 - High
Prickly Sculpin	3 - High	4 - High	Grass Carp	2 - Medium	4 - High
Largemouth Bass	3 - High	3 - Medium	Mississippi Silverside	3 - High	2 - Low
Green Sunfish	3 - High	3 - Medium	Bluefin Killifish	1 - Low	3 - Medium
Black Bullhead	3 - High	1 - Very Low	Red Shiner	1 - Low	2 - Low
Mollusks established			**horizon**		
Italian White Snail	3 - High	3 - Medium	New Zealand Mudsnail	3 - High	2 - Low
Quagga Mussel	3 - High	2 - Low	Zebra Mussel	3 - High	2 - Low
Channeled Apple Snail	1 - Low	3 - Medium			
Decollate Snail	2 - Medium	1 - Very Low			
Herps established			**horizon**		
American Bullfrog	3 - High	4 - High	Sonoran Spotted Whiptail	2 - Medium	4 - High
African Clawed Frog	3 - High	3 - Medium	Rio Grande Leopard Frog, Southern Leopard Frog	2 - Medium	4 - High
Red-eared Slider/Painted Turtle	2 - Medium	4 - High	Banded Water Snake, Northern Water Snake	2 - Medium	2 - Low
Italian Wall Lizard/Green & Brown Anole	2 - Medium	4 - High			
Barred Tiger Salamander	2 - Medium	4 - High			
Arthropods established			**horizon**		
Big-headed Ant/Red imported Fire Ant	3 - High	5 - Very High	Yellow Crazy Ant	3 - High	4 - High
Crayfish	3 - High	4 - High	Electric Blue Crayfish	3 - High	4 - High
Goldspotted Oak Borer	3 - High	3 - Medium	Pine Shoot Beetle / Ambrosia beetles	3 - High	3 - Medium
Shot Hole Borers	3 - High	2 - Low	Asian Long-horned Beetle	3 - High	3 - Medium
Argentine Ant	3 - High	2 - Low			
Mammals established			**horizon**		
American Beaver	3 - High	5 - Very High	Red Fox	3 - High	4 - High
Fox Squirrel	3 - High	4 - High	Nutria	3 - High	3 - Medium
Wild Boar	3 - High	4 - High	Small Indian Mongoose	3 - High	2 - Low
Feral Cat	3 - High	3 - Medium	Ferret	1 - Low	4 - High
House Mouse	2 - Medium	1 - Very Low			

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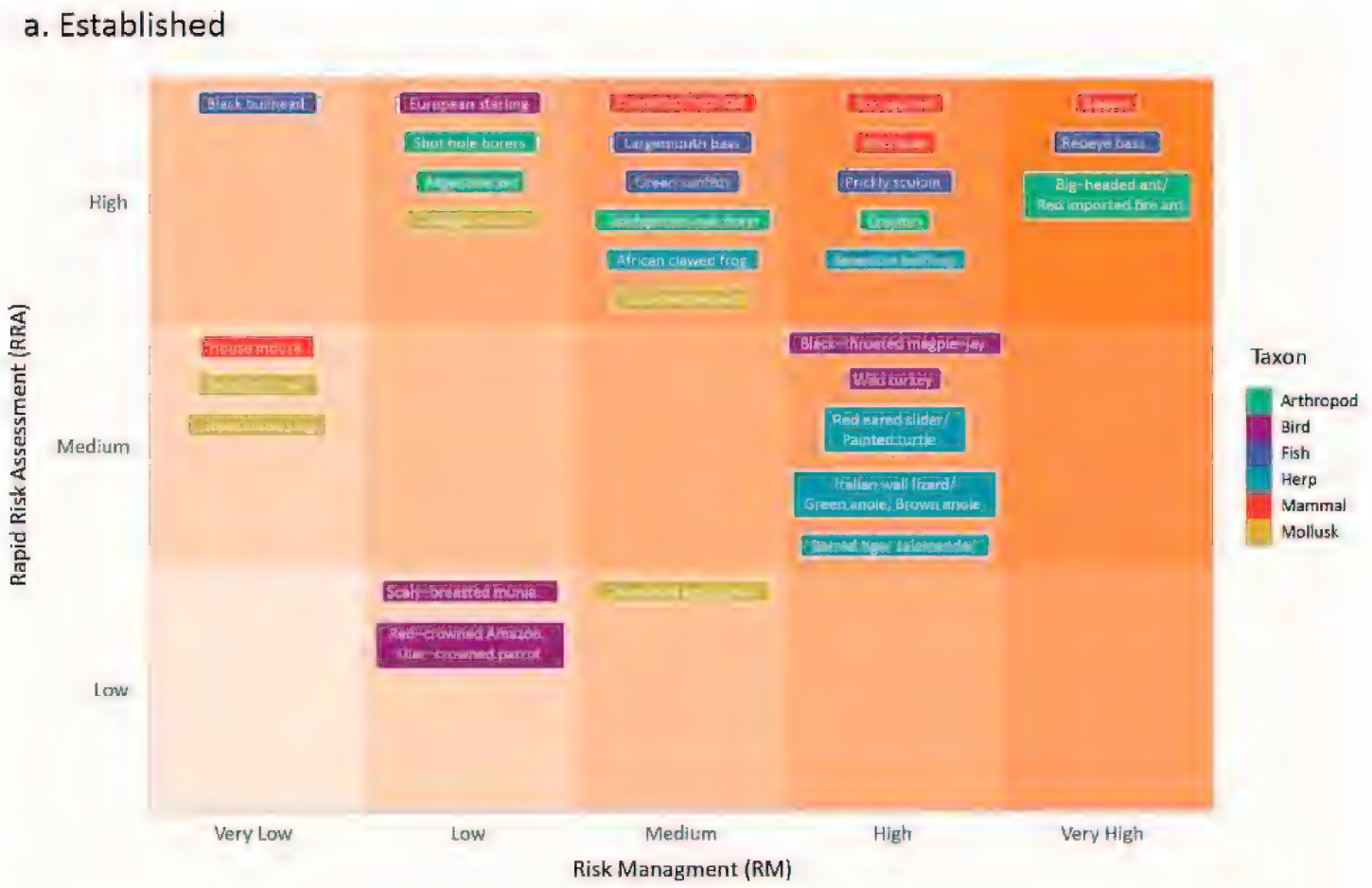

Fig. 3. Heat matrices representing the risk posed by and the feasibility of managing established (a) and horizon species (b). Background shade color of the cells indicates priority (from dark = highest, to light = lowest). Placement within the matrices is based on the RRA and RM sub-ranks for each species.

with previous assertions that greater consistency in the objectives and implementation of invasive species risk analysis among researchers worldwide stands to improve the ways in which we manage invasive species (Brunel et al. 2010; Booy et al. 2017; Roy et al. 2017; Booy et al. 2020). Building on the NNRM model in this study adds to this endeavor and

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Table 4. Means x and standard deviations s of the rapid risk assessment (RRA) and risk management (RM) sub-ranks for established and horizon species. Mollusks were the only group with a single horizon species.

	Established				Horizon			
Taxa	RRA_x	RRA_s	RM_x	RM_s	RRA_x	RRA_s	RM_x	RM_s
Mammals	3.8	0.4	3.4	1.5	3.5	1.0	3.3	1.0
Fish	4.0	0	3.2	1.5	3.0	1.0	3.0	1.0
Herps	3.3	0.5	3.8	0.4	3.0	0	3.3	1.2
Birds	2.8	0.8	2.8	1.1	2.8	0.8	3.6	1.5
Arthropods	4.0	0	3.2	1.3	4.0	0	3.5	0.6
Mollusks	3.2	0.8	2.0	1.0	4.0	–	2.0	–
All Taxa	3.5	0.7	3.1	1.2	3.3	0.8	3.3	1.0

made practical sense for rapidly identifying which non-native species merit the greatest attention in the San Diego County NCCP/HCP reserve system.

The risk rankings for the top-5 species in all taxonomic groups were generally consistent in terms of the threat they pose, whereas the management rankings were considerably more variable (Table 4) – those that were high risk but had low probability for control fell in the rankings, whereas those that could be eradicated or managed to some degree were elevated. This in turn led to final rankings that were driven by management feasibility (Table 3). We recognize that the significance of management feasibility arises in part because only the top-5 highest risk species progressed to the second stage of the analysis; however, this same finding has been shown in other geographic areas that have applied the NNRM protocol (Booy et al. 2020) and intuitively the pattern makes sense.

Table 5. Changes in the rankings for established and horizon species as a result of workshop deliberation. (A) Values reflect changes in the RRA/RM sub-ranks from the discussions within groups on Day 1 and the final consensus on Day 2 (i.e., after deliberation within *and* among groups). 'Taxon rank change' is the percentage of taxa that changed in their position from Day 1 to Day 2 of the workshop. (B) Proportion of all rank changes to invasive species priorities. An upward change indicates an increase in perceived risk, as rank changed to a lower number; a downward change indicates a decrease in perceived risk, as rank changed to a higher number.

A.

Taxa	RRA change	RM change	Taxon rank change
Mammals	11%	11%	44%
Fish	20%	50%	90%
Herptiles	22%	100%	33%
Birds	20%	10%	90%
Arthropods	11%	33%	56%
Mollusks	50%	83%	33%

B.

All taxa	RRA change	RM change	Taxon rank change
Rank change up	19%	25%	32%
Rank change down	2%	21%	28%
No rank change	79%	55%	40%

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Management potential had a somewhat counterintuitive influence on the prioritization of horizon species, given that those identified as high risk but with low management potential (i.e., seemingly the most concerning and unwanted type of horizon species) were assigned moderate rather than high priority as might have been expected. The high-priority argument follows that early detection should lead to better prospects for containment simply because the spread is still limited (Anderson 2005). However, for several species in this study (i.e., Small Indian Mongoose, Mississippi Silverside, New Zealand Mudsnail, and Zebra Mussel), the window of opportunity for containment was considered to be so small that by the time they are detected, their spread would surpass the level at which interdiction could achieve success (although eDNA tests show promise for early detection of New Zealand Mudsnail; Goldberg et al. 2013).

We refer readers to the Supplemental File for summaries on each taxonomic group (Supplemental File taxon_highlights) but briefly discuss a few species here due to their high prioritization in the overall analysis. American Beaver (*Castor canadensis*) ranked high because it was deliberately introduced into the assessment area in the mid-20th century, creates preferred habitat for other non-native predators and competitors to the detriment of native species, has a limited distribution, and is easily detected in the wild (Richmond et al. 2021). We note that previous authors have argued that American Beaver are native to San Diego County (Lanman et al. 2013), but no compelling, verifiable evidence exists that they ever were (see reviews in Richmond et al. 2021). Red-eyed Bass (*Micropterus coosae*) also ranked high because of its potential for containment. The Big-headed Ant (*Pheidole megacephala*) and Red Imported Fire Ant (*Solenopsis invicta*) were unusual in that they straddled the horizon and established (reported but undetermined) categories. Both have been documented transiently in San Diego County and may exist in areas where they have yet to be detected. Because the risk of introduction is persistent, the damage they could impose is severe, and containment relies on early detection (Porter and Savignano 1990; Holway et al. 2002), assessors agreed that both should be regarded as high priority species.

Deviations from the NNRM risk analysis protocol.—We note some minor deviations from the original NNRM protocol that accounted for issues that were unique to this assessment. The first involved time-saving steps (described in 'Supplemental File_protocol_mods') that allowed us to curtail the high number of candidate species yet still focus on those posing the highest risk with some potential for control. A second deviation was that management outcomes emphasized control over eradication because the latter was considered impractical for nearly all established non-native species, and assessors agreed with previous assertions that some level of control offers benefits over no management whatsoever (Hoffmann 2010; Gaigher et al. 2012). It was also suggested that even finer subdivisions within the control category, one that accounts for local versus regional control, might fine-tune the prioritization. An example of a species that could potentially be treated more effectively using this distinction is the American Bullfrog (*Rana catesbeiana*), which may be eradicable in parts of a watershed or possibly even a whole watershed, but not on all conserved lands within the NCCP/HCP (Nicholson et al. 2020).

Challenges of administering a 'one-size fits-all' approach to non-native species risk assessments.—Even with the flexibility of the NNRM protocol, we still encountered issues that required case-by-case evaluations to make final decisions. This was unavoidable due to differences in the invasion biology of a wide variety of taxa, but the rationale underlying these decisions can be easily traced in the RRA and RM templates. We focus on a few of the most noteworthy challenges below and discuss others of less concern in the supplemental materials ('Supplemental File taxon_highlights').

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One challenge involved 'urban-established' species, which were generally de-prioritized because they pose less of a threat to core conservation areas. Two examples were the Domestic Cat (*Felis catus*) and the House Mouse (*Mus musculus*), where both species favor urban areas over the surrounding natural habitat due to nutritional subsidies and lower predation pressure (Davis 1957; George 1974; Warner 1985; Ordeñana et al. 2010). However, the risk of these species increases with closer proximity to the coast, where conserved lands tend to be smaller, more isolated, and more encompassed by development compared to inland areas, where patches are larger, more interconnected, and have less of an interface with the urban environment (Bolger et al. 1997; Crooks and Soulé 1999; Chase et al. 2000; Achury et al. 2021; Ordeñana et al. 2010). This suggests that the risk and management feasibility of certain species is best evaluated with respect to location within the overall landscape.

Alternatively, while the Eastern Fox Squirrel (*Sciurus niger*) is mostly limited to urban areas (King et al. 2010; Muchlinski and Garcia 2017), its capacity to use corridor habitat to expand eastward away from the coast (King 2004; Tremor et al. 2017; Creley et al. 2019), combined with its known potential to displace the native Western Gray Squirrel should the two come into contact (*Sciurus griseus*; Muchlinski et al. 2009; King et al. 2010;), meant that alternative criteria were necessary to adequately prioritize the threat. San Diego is known for its extensive canyon system that interdigitates with the urban matrix, and in some areas connects to larger core habitat (Suarez et al. 1998; Crooks 2002). If the Eastern Fox Squirrel was to infiltrate these corridors, it is plausible that it could extend its range into NCCP/HCP preserves where it could compete with the Western Gray Squirrel and-or the California Ground Squirrel (*Spermophilus beecheyi*). In fact, it has already begun to do so in at least one part of the county in the lower San Diego River in the City of Santee (Tremor et al. 2017). Like the feral Domestic Cat, however, workshop experts noted that public opposition to lethal management would likely be high, particularly in the urban areas.

Flight was another issue that required broadening of the definition of 'horizon' for birds to include certain species that assessors felt were serious threats. Our stated definition was that horizons must be recorded from an adjacent county or from northern Baja California; however, volant species have greater movement capacity than do terrestrial species, so this definition may be too restrictive for birds. For example, while the Nanday Parakeet (*Aratinga nenday*) is established in the non-adjacent counties of Los Angeles and Ventura to the north (Garrett 2018), its potential to reach San Diego County through incremental movement was viewed as too significant for it to be dismissed as a threat to native birds.

Future Directions.—SDMMP and land managers can decide how to use the species rankings reported here. We suggest that focusing on the species ranked highest in priority, which include those that are eradicable and/or have negative ecosystem-wide impacts, may be most beneficial. Targeting these invaders has the potential to lead to the recovery of native species and habitat with limited or perhaps no further intervention, other than maintaining vigilance for new introductions. Removal of non-native species with polytrophic effects could also reduce synergistic interactions among invaders that intensify their impacts and promote secondary invasions (i.e., invasion meltdown; Green et al. 2011).

A follow-up risk analysis could also be expanded to include the next tier of taxa beyond the top-5 posing the greatest risk, a process that might change the prioritization reported here. Our decision to have equal representation across groups in this study was intended to reduce cost, time, and effort in this initial assessment while covering a breadth of the animal diversity in San Diego County. Further application of a structured protocol for

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the consensus building step, such as the IDEA protocol of Hemming et al. (2017), may also help to refine decisions by reducing contextual bias and increasing the transparency of expert judgements.

Assessors suggested that a curated web interface in the spirit of Wikipedia could be developed for the species list and RRA/RM templates with additions or modifications made on-line, and so that the database could be publicly available. This would promote transparency and create an e-trail to the source of the edits. In such a scenario, changes to rankings or the overall prioritization could require input from multiple experts and a consensus among them. In the interim, the USGS has developed the 'San Diego Invasive Species Watch' web portal on iNaturalist.org, which continues to operate and accumulate data on the region's non-native species (www.inaturalist.org/projects/san-diego-invasive-species-watch). Users can view maps of species distributions and determine whether records might constitute incipient invasions or range extensions. The iNaturalist application has built-in checks on identifications such that none rely solely on decisions made by the person who generated the record, and taxonomic experts can verify the record (Theobald et al. 2015; Vendetti et al. 2018; Johnson et al. 2020). We also view it as an educational tool that could be used to engage local elementary and high school students, where awareness about the impacts of invasive species may be lacking.

Conclusions

Our findings highlight the importance of management feasibility (controlled or eradicated) in prioritizing how resources can be used to combat non-native species, rather than solely relying on the inferred risk that any one species poses. In applying this protocol, we prioritized species with the following key characteristics: (1) those producing hierarchical trophic effects that facilitate invasional meltdown; (2) those that can be managed simultaneously using the same control techniques; (3) those with high damage potential that have yet to establish, but for which vigilance is necessary to prevent their establishment; and (4) those for which risk level and management feasibility varies depending on location within the assessment area.

We found the NNRM protocol to be flexible in its application across species, and it was easily tailored to conditions in the Southern California/Northern Baja California coastal ecoregion. Assessors widely agreed that the protocol's reliance on taxonomic expertise and consensus-building provided a 'real time' peer-review process that translated to greater efficiency in achieving the final prioritization, whereas spending time and resources to formulate an arbitrary, quantitative approach for such a wide variety of animal taxa would have been less productive. The framework that now exists can be easily expanded or modified as new threats arise, contrasting opinions weigh in, or as existing invaders are brought under control.

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Live-trapping of Rodents in Urban Green Spaces across Los Angeles

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Abstract.—Urban green spaces have the potential to function as multi-benefit spaces, for both human enjoyment and sustaining native wildlife populations. In our study, we trapped for small nocturnal mammals across a series of Los Angeles green spaces. Our results show that native rodents are only present in habitats that support native vegetation; in particular we highlight the native rodent biodiversity on Sage Hill, a coastal sage scrub remnant on the UCLA campus. Other urban parks that are composed of non-native grasses and non-native shrubbery yielded only invasive species of rodents, including Brown Rats (*Rattus norvegicus*) and House Mice (*Mus musculus*). Our study points to the ability of renovated green space in Los Angeles to support native fauna. In addition, our study demonstrates some of the difficulties in doing trapping studies in heavily urbanized environments.

In our study we used live trapping to investigate whether green spaces across Los Angeles support native rodent populations, and what factors might affect the presence of native versus introduced small mammal species. "Green spaces" are often thought of, and sold to the public, as tools for conservation of local fauna in metropolitan areas (Ofori et al. 2018). The 2016 Los Angeles Countywide Comprehensive Parks and Recreation Needs Assessment, written by Los Angeles County Department of Parks & Recreation[1], states that Los Angeles parks built or renovated in the future should be 'multi-benefit', not only for human enjoyment but also contributing to the enhancement of regional sustainability and provision of ecosystem services. Testing whether local fauna use metropolitan green spaces is key to future planning, both as a tool for conservation and for popularizing conservation efforts.

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Sage Hill at the University of California, Los Angeles (UCLA) is the last patch of natural coastal sage scrub vegetation on campus[2], and in fact in the entire area of west Los Angeles south of Sunset Boulevard. It has been promoted as a haven not just for the natural flora of the area, but also the fauna. In 1996 a UCLA Geography course[2], performed an inventory of the vegetation, birds, herpetofauna, arthropods, and mammals at the site. In their small mammal inventory, both native and invasive rodents were trapped at Sage Hill, including two Big-Eared Woodrats (*Neotoma macrotis*), one Brown Rat (*Rattus norvegicus*), and two House Mice (*Mus musculus*), as a result of trapping efforts of 32 traps on two different nights. The 1996 trapping success rate varied from 6.25% to 15.6% trap success on the two nights of capture.

In comparison, similar trapping methods and efforts at a continuous area of similar habitat, Leo Carrillo State Beach, yielded a lower number of species but much higher trapping success, and a higher proportion of native species trapped[2]. Another local study that catalogued small mammals was carried out in 2000 in the Baldwin Hills area of Los Angeles by Dines[3]. This area retains native vegetation and also contains large preserved green spaces, e.g., Kenneth Hahn State Park, as well as much of the current oil exploitation in the Los Angeles Basin (Fig. 1). The Baldwin Hills study included live-trapping of nocturnal small mammals. Four nights of trap-lines were set, and four species of rodent were trapped, including one invasive species, the House Mouse, and three native species to southern California, the California Pocket-Mouse (*Chaetodipus californicus*), the California Vole (*Microtus californicus*), and the Big-Eared Woodrat, with a success rate for trapping efforts at about 20%. The current project began as an effort to provide a new inventory of the small mammals at Sage Hill twenty years after the 1996 survey, and later expanded to inventory green spaces across urban Los Angeles for nocturnal small mammals.

Materials and Methods

In a pilot study to catalogue small nocturnal rodent species presence on Sage Hill, on the northwestern corner of the UCLA campus, a trapping program was carried out in Spring 2015 and in Spring 2016 by the first author (ARF) and students for the UCLA GE70C seminar, "Evolution: A Naturalist's Perspective" (a full list of students from the 2016 course is provided in Acknowledgments). Sage Hill is bounded on the west by Veteran Avenue and on the east by the residence halls along De Neve Drive. Three nights of trapping were performed on Sage Hill during each class. In each case, fifty traps were set in 3 trap lines, mainly on the south end of Sage Hill, starting from the bottom of the hill and ending at the top of the hill near the fencing that separates Sage Hill from the residence halls. Traps were set about 3 m apart, although this was modified based on local terrain and vegetation. Sherman-style live traps (7.62 × 8.89 × 22.86 cm) were used to allow for capture-and-release of animals (Hoffman et al. 2010). Trap size was selected to allow for the largest rodents (rats) to fit but to prevent larger animals (e.g., rabbits or foxes)

[2] Mattoni R., Angulo A., Burnam J., Chalekian J., Chen J., Cortez N., Duvernay E., Farris C., Fry D., Hill R., Hillway K., Post A., Pun, K., Scholnick J., Sway D., Varvel, A., Wilson G., and Yancey C. 1997. Biological Assessment: Coastal Sage Scrub at University of California, Los Angeles. Geography 123: Bioresource Management UCLA Department of Geography, Winter 1996, Longcore T., Mattoni R., Maldonado J., Hertel F., Scow J., eds. Los Angeles, CA.

[3] Dines J.P. 2001. Mammals of the Baldwin Hills. The Biota of the Baldwin Hills: An Ecological Assessment. Pp. 127–141 in Community Conservation International and Natural History Museum of Los Angeles County (Molina KC, ed.), Los Angeles, USA.

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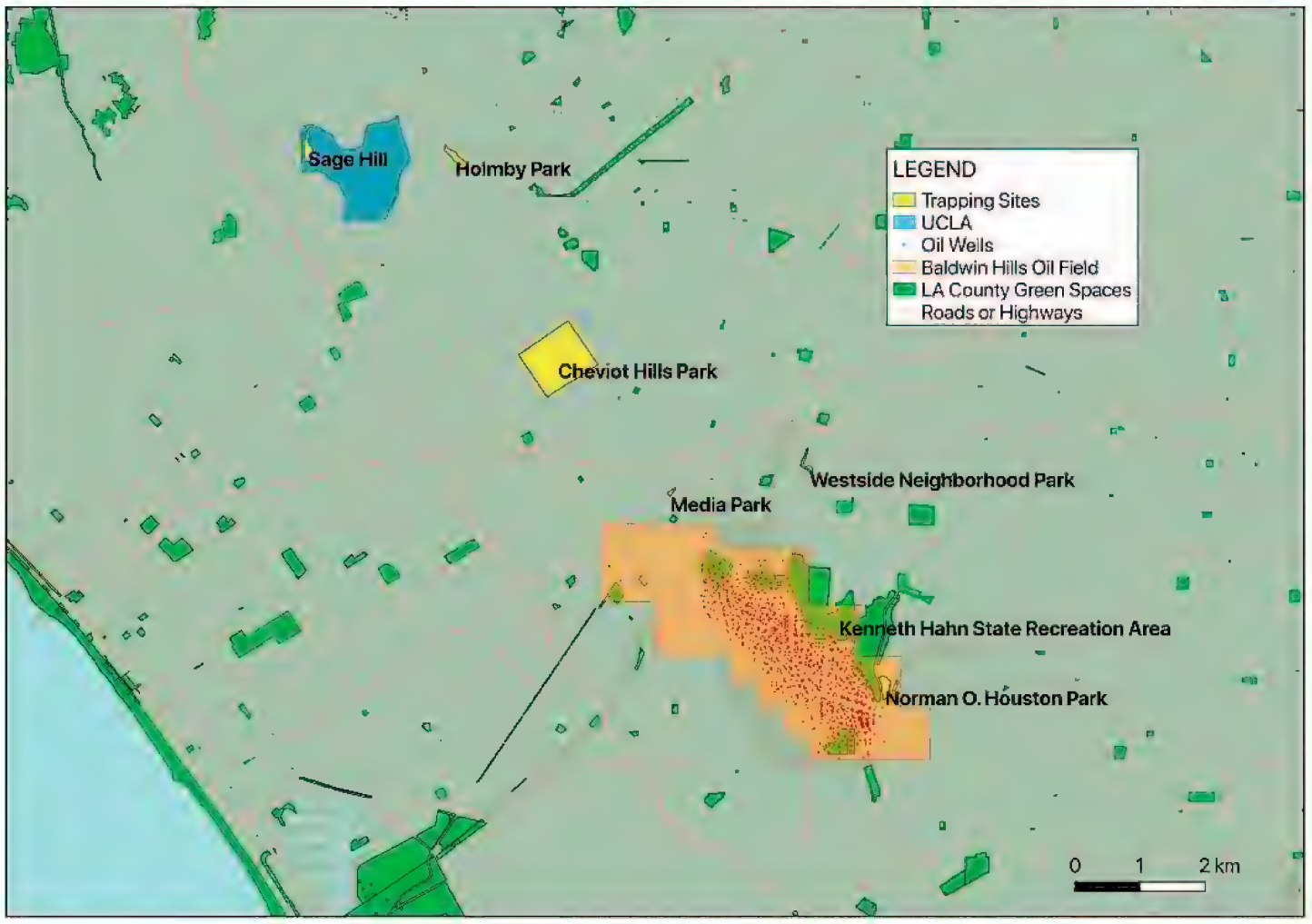

Fig. 1. GIS Image of western Los Angeles. Location of trapping sites and other localities mentioned in the text are shown. North is towards the top. Image created using QGIS (QGIS Development Team, 2020) and open-source L.A. city and county GIS datasets.

from being able to enter. Traps were baited with a combination of oats (Hoffman et al. 2010; Brehme et al. 2011), peanut butter (Hoffman et al. 2010), and diced apple (Frye et al. 2015). Raw cotton was added to each trap to allow for nesting and help alleviate any effects of cold weather at night (Wilson et al. 2007). All traps were closed during the day, baited just before sunset, and checked soon after sunrise. All specimens were handled according to UCLA Office of Animal Research Oversight protocols (protocol #2015–052–01). Upon verification of an occupied trap, the trap was inverted into a clear, plastic bag, which allowed for identification to species (Reid 2006) prior to release. While marking or tagging of trapped individuals would have been ideal, this was not permitted in this pilot study.

The success in the pilot study of documenting native small mammals on the UCLA campus became the impetus for a larger study to investigate the presence of rodents, especially native species, at other "green spaces" across the Los Angeles urban landscape that include little, if any, native vegetation. In 2018 trapping was carried out at Los Angeles City Parks (with permission from park officials) and trapping also was repeated at Sage Hill. Trapping was performed under scientific collecting permit SC-13720 from the California Department of Fish & Wildlife and all animal handling carried out by ARF in accordance with procedures laid out by the UCLA Research Safety & Animal Welfare Administration (ARC# 2015-052-01). Funding for the 2018 study was through UCLA Grand Challenges: Sustainable Los Angeles, under the Urban Ecology of Los Angeles Mammals grant. Several undergraduate students at UCLA took part in the trapping effort as student interns and volunteers.

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Table 1. Trapping locations, areas and dates in 2018.

Locality	Area (ha)	Trapping dates (all 2018)
Sage Hill (SH)	1.51	4/24-4/27
		8/28-9/31
Holmby Park (HP)	4.35	5/29-6/1
		10/2-10/5
Westside Neighborhood Park (WNP)	1.43	6/5-6/8
		10/9-10/12
Media Park (MP)	0.68	7/17-7/20
		10/23-10/26
Norman O. Houston Park (NOHP)	2.92	7/31-8/3
		11/6-11/9
Cheviot Hills (CH)	10.9	8/14-8/17
		11/13-11/16

Trapping occurred at five Los Angeles city parks as well as Sage Hill (Fig. 1 and Table 1). Parks were chosen based on the presence of enough vegetation to allow for placement of traps. Parks ranged in size from 0.68 ha to 10.9 ha, and other than Sage Hill were mainly groomed spaces with lawns and introduced shrubbery, and very little native vegetation or ground cover over cut-grass height, as is typical of Los Angeles parks. We performed two trapping sequences of three nights each at each location. One set of trapping sequences spanned late spring through early summer of 2018, and the other the fall of 2018. Each night, 30 traps were set in trap-lines, with traps set in the same places each night. Trapping protocol in 2018 was the same as described above for the 2015-16 Sage Hill trapping effort. More information about specifics of where traps were set is available upon request.

Results

In Fall 2015, three nights of trapping at Sage Hill did not result in the capture of any small mammals (see discussion). In 2016, over the course of 150 trap nights (50 traps over 3 nights) at Sage Hill, nine animals were captured (a success rate of 6%). Five different species were captured, out of which four were southern California native species: Deer Mouse (*Peromyscus maniculatus*), trapped on 2 nights; California Vole, trapped on two nights; Big-Eared Woodrat, captured on three nights (but may have been the same individual on different nights, given the woodrat nest near to the trapping site); and California Pocket-Mouse (*Chaetodipus californicus*), trapped on one night. The diurnal California Ground Squirrel (*Otospermophilus beecheyi*) commonly are observed on Sage Hill, bringing the total number of native rodents up to five. The only invasive species captured was the House Mouse. Neither the Black Rat nor the Brown Rat was captured, although rats are commonly observed in other parts of the campus.

Across all Los Angeles green space sites and all trapping sequences in 2018, there was a total of 1080 'trap nights', and a total of 29 captures, for a trapping success rate of 2.7% (Table 2). The low number of 'free lunches' during the study, where bait was missing without the trap being sprung, indicates that the traps were typically sprung if an animal entered them. Trapping success rate varied across sites and trapping sequences. For example, trap success rate at Cheviot Hills was 11% in the spring, but 0% in the fall. Although the lunar cycle is known to affect small mammal activity patterns (Owen et al., 2021), we did not attempt to correct for this as most parks were lit throughout the night and there seemed to

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Table 2. Trapping success and animals trapped by locality in main study.

Locality	Trapping dates	# of Animals captured	Black Rat	House Mouse	Big-Eared Woodrat	Undetermined
SH	4/24-4/27	1			1	
HP	5/29-6/1	3		3		
WNP	6/5-6/8	0				
MP	7/17-7/20	2	2			
NOHP	7/31-8/3	2		2		
CH	8/14-8/17	10	9	1		
SH	8/28-8/31	1				1
HP	10/2-10/5	1	1			
WNP	10/9-10/12	0				
MP	10/23-10/26	0				
NOHP	11/6-11/9	9		9		
CH	11/13-11/16	0				
TOTAL		**29**	**12**	**15**	**1**	**1**

Abbreviations for localities follow those in Table 1.

be no correlation of trapping success and lunar phase. Of the animals captured throughout the main study across Los Angeles parks, only two were native California species (Big-Eared Woodrat and Deer Mouse), and these were both captured at Sage Hill (see Table 2). No native species were captured in city parks, not even at Holmby Park, a park of a similar distance to the Santa Monica Mountains as Sage Hill, nor at Norman O. Houston Park, a park very close to Baldwin Hills, an area with extensive native vegetation where a previous trapping study revealed several species of native small mammals.

The species captured at Sage Hill across the different years of study were the more common nocturnal small mammals in Southern California. The Deer Mouse is probably the most widespread native mouse in North America (Reid 2006) (but see Kalkvik et al. 2012 for alternative taxonomy). The cover provided by the vegetation at Sage Hill, and the presence of some shrubbery and trees, provide the perfect habitat for the mice. It is unknown whether the mice range across the entire campus. The Big-Eared Woodrat was captured every night in the 2016 trapping, and was captured again in 2018. A woodrat nest is present near the area where it was consistently captured, and its presence has been noted at Sage Hill before. Our trapping area at Sage Hill probably only has enough acreage to support one woodrat individual (Innes et al. 2012), although the entire acreage of Sage Hill has a number of woodrat nests. The California Vole is another common species, present throughout wetter habitats in California (Kalkvik et al. 2012). The grass cover in the trapping area at Sage Hill makes it a suitable habitat. It would be interesting to determine if voles are prey species for local predators as they are a key prey species in native habitats (Kalkvik et al. 2012). One small native mouse caught at Sage Hill was unable to be identified before it escaped handling. A tentative identification is a California Pocket-Mouse. The California Pocket-Mouse has been recorded in the Santa Monica Mountains, so it would not be surprising to find it at Sage Hill, but its presence should be confirmed with further trapping.

Invasive species captured at Sage Hill across our study were limited to one House Mouse in 2016. Across all the Los Angeles green spaces with non-native vegetation that we sampled for trapping small mammals, we captured only invasive species, including rats and House Mice (Table 2).

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Discussion

Our 2016 trapping effort done as part of a UCLA undergraduate class project demonstrated the presence of multiple native small mammal species on Sage Hill, a relatively isolated patch of native habitat. Prior to trapping, we expected to capture a number of individuals of invasive species, like the house mouse and the black or brown rat which are commonly seen across campus, and are often pests in buildings. The fact that we did not catch many invasive species at Sage Hill speaks to a possibly important role for the patches of natural habitat in urban settings. They could act as important refuges for native species. Further trapping should be done elsewhere on campus to find out if the native rodent species are found across the UCLA campus, or only in this preserved habitat. This could be done with the help of campus pest control, who could provide information on the individuals they capture. This also raises the question of how much connection Sage Hill has to larger populations of native species in the Santa Monica Mountains. The only way to address this would be a more in-depth study involving the population genetics of Sage Hill and nearby mountain areas and/or tracking studies of individuals found at Sage Hill.

Studies conducted in cities around the world have found that native species compose only a small minority of the flora found within urban green spaces (Bolger et al. 1997; Figueroa et al. 2018). This makes Sage Hill, where California natives make up nearly 100% of the flora in some vegetative patches, especially unique[4]. In general, species richness is reduced in areas of extreme urbanization (McKinney 2008). Invasive species, which spread more easily in urban settings, can cause significant ecological imbalances, disrupting beneficial ecosystem services, such as energy, nutrient, and water cycling, that humans often depend upon (Charles and Dukes 2007). Near-natural habitats are better equipped to resist the establishment of invasive species (Gong et al. 2013). Therefore, protecting and expanding relatively undisturbed habitats, like Sage Hill, is crucial for improving the biodiversity and ecosystem services available in urban settings. Our study suggests that, despite being far removed from other coastal sage scrub habitats, this relatively small area was still better suited to harbor native rodents than larger, more artificial green spaces. In addition, Sage Hill's location on the UCLA campus makes it an invaluable resource for the academic community. The site resembles much of the surrounding area prior to urban development[4], and thus allows for an understanding of southern California's ecological history. Sage Hill already has been the site of multiple undergraduate class projects, and the present study afforded several undergraduate students early research experience. Protecting Sage Hill not only makes invaluable knowledge accessible to students and researchers, but also preserves a model to inform the design of future Los Angeles parks.

Our Fall 2015 trapping effort at Sage Hill yielded no captures of small mammals, but the same amount of trapping effort in Spring 2016 yielded four species of native taxa. The main difference between the two times was that in fall, all the non-native grasses had been cut, so there was very little cover in the area. Cover, native or otherwise, is an important driver of rodent occupancy of an area.

[4] Mattoni R., Angulo A., Burnam J., Chalekian J., Chen J., Cortez N., Duvernay E., Farris C., Fry D., Hill R., Hillway K., Post A., Pun, K., Scholnick J., Sway D., Varvel, A., Wilson G., and Yancey C. 1997. Biological Assessment: Coastal Sage Scrub at University of California, Los Angeles. Geography 123: Bioresource Management UCLA Department of Geography, Winter 1996, Longcore T., Mattoni R., Maldonado J., Hertel F., Scow J., editors. Los Angeles, CA.

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We expected some relationship between the presence of native animals to the size of the park or proximity to native habitats (Bolger et al. 1997), however neither relationship was observed. Holmby Park is situated a similar distance to the Santa Monica Mountains as Sage Hill (~1 km), but no native species were captured. Similarly, Norman O. Houston Park is in the Baldwin Hills, much of which is a relatively large green space with native flora and native rodent species, and although the Park had the overall highest trap rate success of the study (6.1%), only invasive species were captured. This park is across a major thoroughfare (La Brea Avenue) from the main area of Baldwin Hills, suggesting that roads with high traffic volume may be enough to block movement of native rodents here (Riley et al. 2006). Since the city parks were all established in the "Late Postwar" period (1957-1975)[5] there is no significant difference in the time they have been isolated which may have contributed to differences in native species presence.

In Los Angeles many city parks have no vegetation; a common type of park is just playground equipment on artificial surfaces. The parks that were 'urban green spaces' chosen for this study had some kind of vegetation, either native or, more commonly, introduced. Some parks did have small, decorative patches of native plants (e.g., Westside Neighborhood Park), but they were not contiguous and the city parks were all dominated by groomed lawns or bare ground and non-native shrubbery. In our study, native rodent species were never captured in these green spaces without native vegetation.

The overall low trapping success rate at the city parks could be attributed to a number of factors. Food in the form of trash was readily available. In addition, most city parks had baited kill traps set by park management for pest control. As described in Desvars-Larrive et al. (2018), trapping difficulty for urban rats can be heightened by food abundance and predator presence (including domestic pets), among other variables such as rodenticide use. Small rodent abundance is also known to fluctuate annually (Blaustein 1981), and in Southern California there tend to be low population sizes in winter and higher population sizes in spring and summer during the breeding season, with summer to early fall the maximum density[6]. In urban environments partnerships with pest control agencies might help yield data unavailable through traditional conservation-based trapping; this avenue is being explored by other members of our research group (Altrudi and Kelty 2022).

Trapping in urban areas leads to a number of other difficulties as well. Although we had permission to trap from the head ranger of the LA City Parks, that information did not always make it to down to 'front line' workers. On one of our first trapping nights, at Holmby Park, we left our traps out (but closed) during the day, and when we came to bait them in the evening, they were all gone. A groundskeeper had taken all of them (and destroyed a few) thinking that they were illegally placed. They were returned to us only after explaining to him what we were doing, and making a call to the head ranger. After this we always removed traps during the day, but replaced them in the same locations each night. Park patrons were also wary of our work. They worried that we were using poisoned bait that could be obtained by children or pets. A key part of the work of rodent

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trapping surveys is the public education component (Desvars-Larrive et al. 2018) and our team engaged in many conversations with the public about our project.

Conclusions

"Green spaces" are often portrayed as wildlife refuges in urban environments. This can only be verified through censusing of wildlife in these spaces. Although birds and some insects could easily move between green spaces and between urban and natural environments, small mammals would almost certainly be more constrained in their movements. In our study, invasive rodent species dominated non-native green spaces across the city. Although preliminary, this study also shows that native small mammal species will take advantage of preserved habitats within an urban environment. In addition, they might outcompete invasive species in these preserved patches, highlighting the importance of native vegetation in preserving local small mammal biodiversity, a key observation that should be considered in future park creation and renovation. We especially want to highlight the unique characteristics of Sage Hill on the UCLA campus, and the importance of protecting this native area. We also want to emphasize the difficulties in trapping in a highly urbanized landscape, as well as the utility of undergraduate coursework that involves local students in cataloguing biodiversity on an urban campus and in the surrounding urban landscape. Future studies will work to increase the sample size as well as utilize proper mark-and-recapture and population genetic methods to better characterize the rodent population in LA green spaces.

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